A New Pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland

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A NEW PACHYPLEUROSAUR (REPTILIA: SAUROPTERYGIA) FROM THE MIDDLE TRIASSIC OF MONTE SAN GIORGIO, SWITZERLAND

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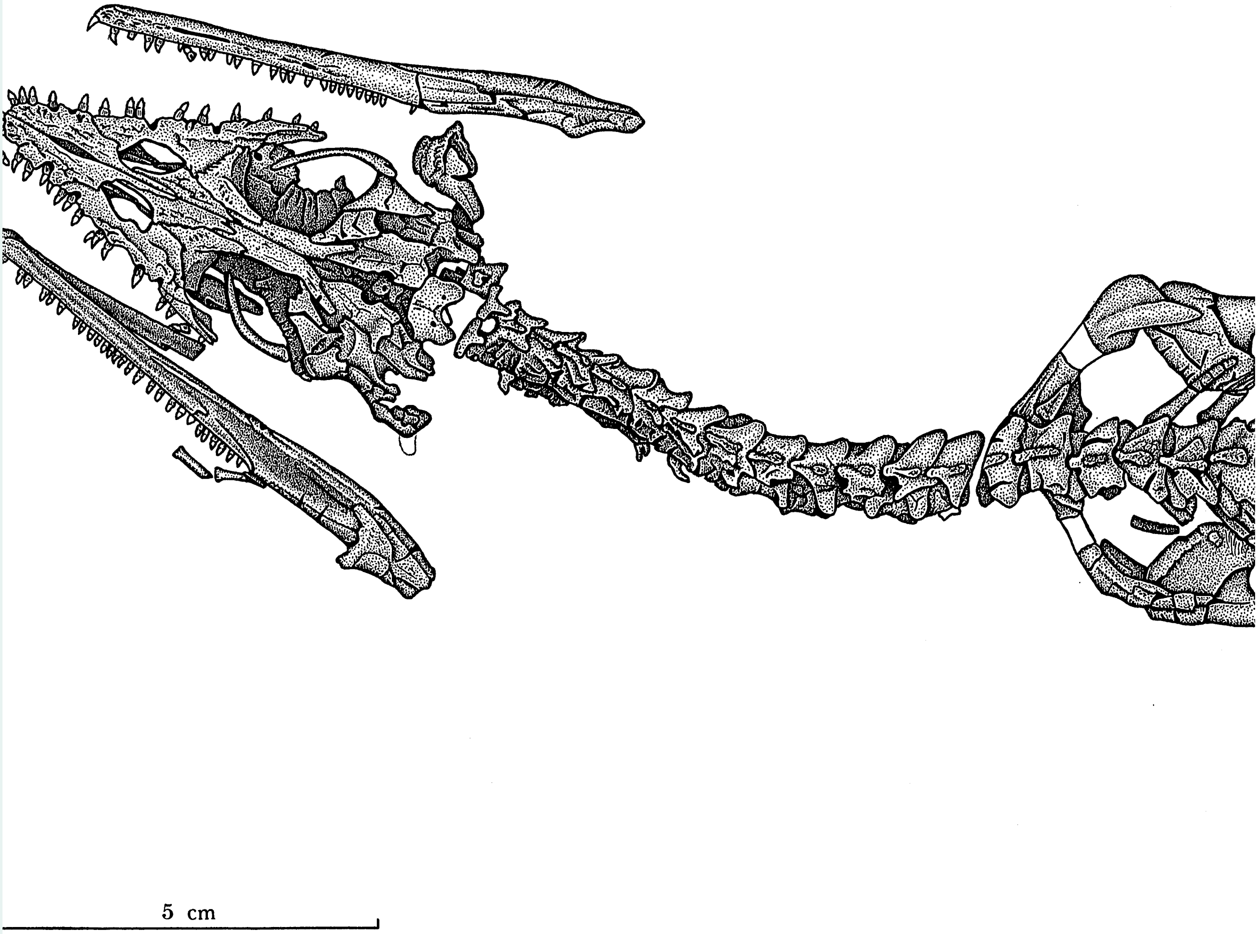
Pachypleurosaur material from the Middle Triassic 'Grenzbitumen'-horizon (Anis–Ladin boundary) of Monte San Giorgio, Kanton Tessin, Switzerland, is described as a new genus and species, *Serpianosaurus mirigiolensis*. A detailed morphological description is followed by a quantitative analysis. The taxon differs from other pachypleurosaurids primarily by its relatively large skull and its straight lower jaw. Rib pachyostosis is absent. In most characters the taxon remains plesiomorphous with respect to other pachypleurosaurs from the Middle Triassic deposits of Monte San Giorgio, which accords well with its early stratigraphic occurrence at that locality. Sexual dimorphism is expressed by the size and shape of the humerus. A cladistic analysis shows the Pachypleurosauridae to constitute the sistergroup of all other Sauropterygia. The Sauropterygia and the Placodontia together form a monophyletic group, the Euryapsida, which is subordinated to the Diapsida and to the Neodiapsida, but which is classifed outside the archosauromorph–lepidosauromorph dichotomy within the Neodiapsida. A concluding paragraph discusses the status of the pachypleurosaurs within the Sauropterygia. Skull structure, and jaw mechanics in particular, suggest a relatively plesiomorph position of pachypleurosaurs within the Sauropterygia. Their adaptation to an aquatic mode of life was not carried to the degree observed in other sauropterygians, and the ability for rapid and deep dives seems to have been limited by middle-ear structure.

Introduction

The first *Pachypleurosaurus* material described came from the Middle Triassic of Besano and Viggiù, northern Italy (Cornalia 1854). Early work on pachypleurosaurs from northern Italy was hampered by the incompleteness of the material, rendering the delineation of pachypleurosaurs from lariosaurs difficult and controversial (Rieppel 1987*a*). The first pachypleurosaurs from the 'Grenzbitumen'-horizon of Monte San Giorgio, Kanton Tessin, Switzerland, were reported by Bernhard Peyer at a meeting in 1928 and described in 1932 (Peyer 1928, 1932). The revision of the lariosaur and pachypleurosaurid material from northern Italy by Peyer (1934) provided evidence for the recognition of the family Pachypleurosauridae, first erected by Nopcsa (1928), and its demarcation from other nothosaurs, including *Lariosaurus*. A larger sample of *Pachypleurosaurus* specimens from the Middle Triassic of Monte San Giorgio formed the basis of Zangerl's (1935) investigation of the osteology and variability of the genus.

After this work, the pachypleurosaurs were not subject to detailed investigations for several decades, although new material was continually collected at Monte San Giorgio. Early on during the excavations at Point 902 a relatively large specimen was found, which after preparation was informally referred to the genus *Phygosaurus* (Arthaber 1924). This specimen is here designated as the type of a new pachypleurosaur genus and species, to which the other material from the 'Grenzbitumen'-horizon (Point 902) will also have to be referred. Within the other, geologically younger pachypleurosaur material from the Tessin, two size classes were recognized; they were interpreted by Kuhn-Schnyder (1974, p. 68) as indicating the presence of a few adults and many schooling juveniles. Carroll & Gaskill (1985), in a monographic revision of *Pachypleurosaurus edwardsii* (Cornalia, 1854), were able to show that these size classes represent two distinct taxa, the larger and geologically younger specimens belonging to the genus *Pachypleurosaurus*, the smaller animals representing the genus *Neusticosaurus*, which is currently under investigation by P. M. Sander.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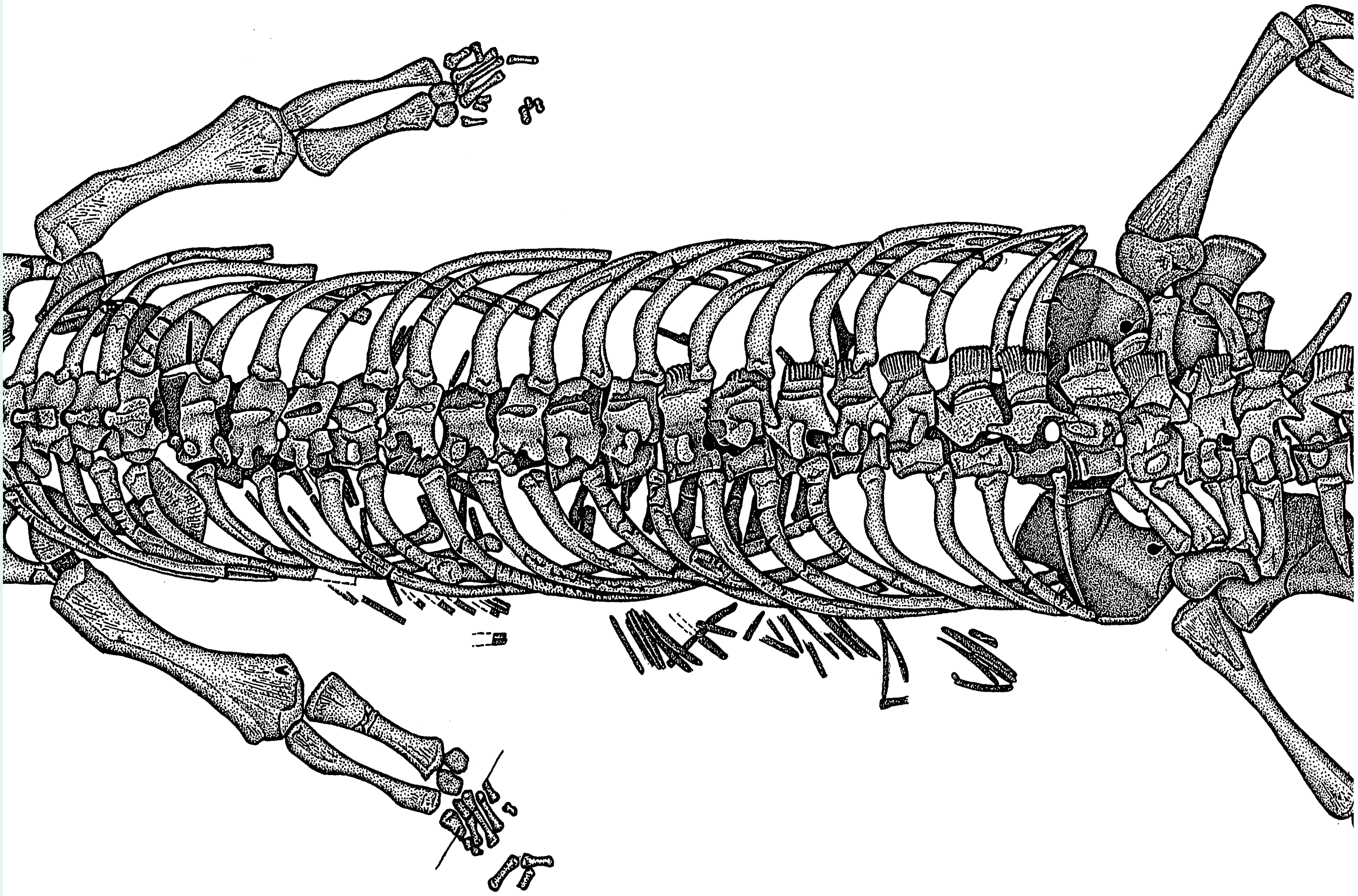

FIGURE 1. The type specimen of *Serpianosaurus m*

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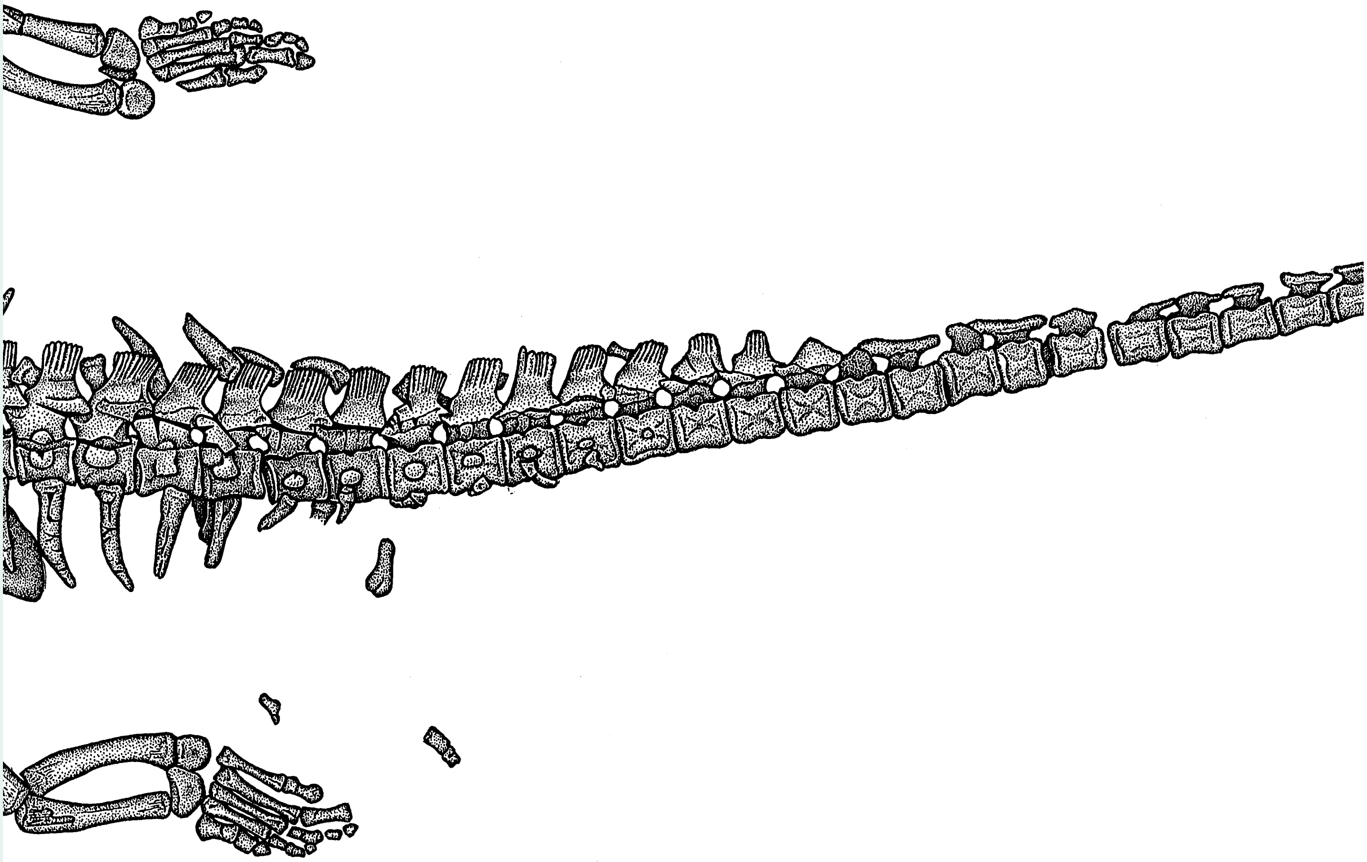
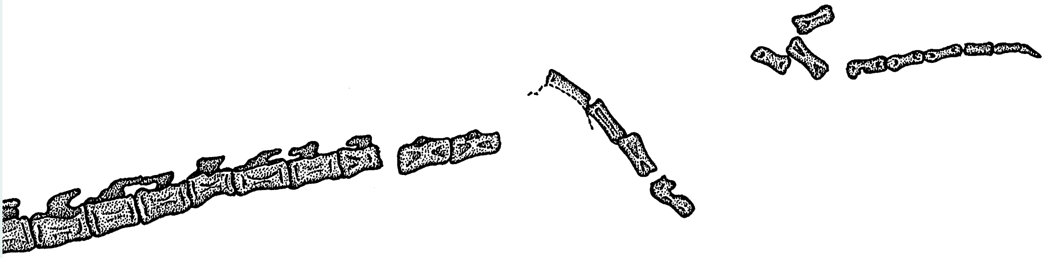


nirigiolensis n. gen. n. sp.



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In the present contribution, the material from Point 902, Val Porina and Cava Tre Fontane, informally referred to the genus *Phygosaurus*, are described as a new genus and species. This is followed by an analysis of phylogenetic interrelationships of the Sauropterygia, and by a consideration of the status of the pachypleurosaurs within the Sauropterygia.

Systematic palaeontology

Eureptilia Olson, 1947
Diapsida Osborn, 1903
Neodiapsida Benton, 1985
Sauropterygia Owen, 1980, p. 209
Pachypleurosauroidea von Huene, 1956, p. 382
Pachypleurosauridae Nopcsa, 1928, p. 43

Serpianosaurus gen. nov.

Type species. *Serpianosaurus mirigiolensis* sp. nov.

Generic diagnosis. An intermediate-sized pachypleurosaur, growing to a total size of approximately 750 mm (glenoid–acetabulum length 187 mm) and hence becoming larger than *Neusticosaurus*, but remaining smaller than *Pachypleurosaurus*. The skull is relatively long, the lower jaw is straight, the upper temporal fossa is oblong with a longitudinal diameter of *ca*. 5.5% (4.8–6.5%) of total skull length. There are 15 or 16 tooth positions on the maxilla, whereas the dentary bears a minimum of 31 teeth. The dorsal ribs are not pachyostotic, the ventral or gastral ribs are composed of five elements each. The scapula bears a distinct ridge separating the areas of origin of the dorsal and ventral pectoral muscles; the medial margin of the coracoid foramen is ossified. The primitive phalangeal formula may be preserved in manus and pes.

Distribution. Middle Triassic ('Grenzbitumen'-horizon, Anis–Ladin boundary); Point 902, Valporina and Cava Tre Fontane, Monte San Giorgio, Kanton Tessin, Switzerland.

Serpianosaurus mirigiolensis sp. nov.

1932 *Pachypleurosaurus edwardsii* Cornalia (partim). – B. Peyer, *Abh. schweiz. paläont. Ges.* **52**: text figs 6 and 7. (The specimen is now catalogued as T 3402.)

1935 *Pachypleurosaurus edwardsii* Cornalia (partim). – R. Zangerl, *Abh. schweiz. paläont. Ges.* **56**: text figs 32, 36 and 44. (The specimens are now catalogued as T 3402 and T 3406.)

Holotype. Paläontologisches Institut und Museum der Universität Zürich, Tessin-collection no. T 3931 (figure 1), Monte San Giorgio, Point 902; further data have been lost. However, the specimen was found and prepared during early phases of excavations at the site Point 902, and it therefore must have come from the upper layers, between nos 140 and 150.

Diagnosis. Same as for genus, of which this is the only known species.

Referred specimens.

T 81	Point 902.
T 96	Point 902.
T 97	Point 902, layer 164, coll. 27 Aug. 1953.
T 132	Point 902, layer 145, coll. 14 Sep. 1955.
T 951	Point 902.
T 1045	Point 902, layer 142, coll. 28 Aug. 1956.
T 1071	Point 902, layer 146, coll. 13 Sep. 1955.
T 1834 a, b	Val Porina, Tetto nuovo, coll. 16 Sep. 1931.
T 3391	No data.
T 3402	Val Porina, Tetto nuovo.
T 3406	Val Porina, Tetto nuovo, Livello frà e cava.
T 3448	Val Porina, Tetto nuovo.
T 3473	Val Porina, Tetto nuovo.
T 3674	Point 902, layer 165, coll. 19 Aug. 1953.
T 3675	Point 902, layer 165, coll. 19 Aug. 1953.
T 3676	Point 902, layer 165, coll. 19 Aug. 1953.
T 3677	Point 902, layer 165, coll. 20 Aug. 1953.
T 3678	Point 902, layer 164o.
T 3679	Point 902, layer 163, 11 Sep. 1953.
T 3680	Point 902, layer 164o, coll. 10 Sep. 1953.
T 3681	Point 902, layer 165, coll. 20 Aug. 1953.
T 3682	Point 902, layer 163, coll. 29 Aug. 1953.
T 3683	Point 902, layer 146, coll. 14 Sep. 1955.
T 3684	Point 902, layer 146, coll. 16 Sep. 1955.
T 3685	Val Porina, coll. 3 Oct. 1956.
T 3709	Cava Tre Fontane, coll. July 1941.
T 3742	Point 902, layer 132.
T 3771	Point 902, layer 145, coll. 16 Sep. 1955.
T 3807	No data.
T 3810	Point 902, layer 146.
T 3931	Point 902.
T 3933	Point 902.
T 4017 X-ray	Val Porina, Tetto nuovo, Livello 9, coll. 18 Sep. 1931.
T 4043 X-ray	Val Porina, Tetto nuovo, Livello 9, coll. 15 Sep. 1931.
T 4076 X-ray	Val Porina, Tetto nuovo, Livello 9, coll. 17 Sep. 1931.
T 4115 X-ray	Val Porina, Tetto nuovo, Livello 8, coll. 1 Sep. 1937.
T 4133 X-ray	Val Porina, Tetto nuovo, Livello 9, Cava 31.

Etymology. The generic name *Serpianosaurus* refers to the village of Serpiano at the foot of Monte San Giorgio close to Point 902. It served as a base for early excavations in the Monte San Giorgio area (Cava Tre Fontane) by B. Peyer (Peyer 1931, p. 5). The specific name *mirigiolensis* refers to an old field name designating Point 902, the locality that has yielded most of the *Serpianosaurus* specimens.

A note on stratigraphical distribution. The oldest fossiliferous layer at the Monte San Giorgio is the 'Grenzbitumen'-horizon, corresponding to the Anisian–Ladinian boundary (Rieber 1973); it yielded pachypleurosaur material here referred to the new genus *Serpianosaurus*. Excavation sites at this stratigraphical level include Point 902, Val Porina and Cava Tre Fontane (Sander 1989). *Serpianosaurus* has come from all three localities, although the material from Point 902 is most abundant.

The deposits of Monte San Giorgio then extend to progressively younger strata through the Ladinian (see Kuhn-Schnyder 1974; Carroll & Gaskill 1985, fig. 10), up to the base of the 'Upper Meridekalke'; the majority of the *Pachypleurosaurus edwardsii* specimens have come from the 'Alla Cascina' of that horizon (Carroll & Gaskill 1985). Kuhn-Schnyder (1987) has recently described a *Lariosaurus* specimen from still younger deposits at Monte San Giorgio, about 50–100 m above the 'Alla Cascina'-horizon; it represents the geologically youngest tetrapod from that locality. The layers between the 'Grenzbitumenzone' and the 'Upper Meridekalke' (Alla Cascina) have yielded the abundant material of 'small pachypleurosaurids', provisionally referred to the genus *Neusticosaurus* by Carroll & Gaskill (1985, p. 349) and currently under investigation by P. M. Sander.

A note on nomenclature. The type specimen of *Serpianosaurus* (T 3931) has long been recognized as a taxon different from the majority of the 'small pachypleurosaurs' now referred to the genus *Neusticosaurus* (Carroll & Gaskill 1985; Sander 1989). Specimen T 3931 was therefore informally referred to the genus *Phygosaurus*, probably on the basis of the redescription of the type of *Phygosaurus* by Peyer (1934). As will be argued in detail below, *Phygosaurus perledicus* (Arthaber, 1934) is a *nomen dubium*, which made it necessary to refer the Monte San Giorgio material to a new genus and species.

MORPHOLOGICAL DESCRIPTION

The skull

General remarks and proportions

The genus *Serpianosaurus* is readily distinguished from all other Pachypleurosauridae from the 'Grenzbitumenzone' of Monte San Giorgio by the size and shape of the lower jaw. The latter shows a straight anterior portion (dentary), and it is relatively longer than in the related taxa.

Among the specimens described in the present study, T 1071 exhibits a nearly three-dimensionally preserved skull that is only slightly distorted; this permits the reconstruction of the outlines of the skull. This specimen is characterized by a straight lateral margin of the facial region of the skull (maxilla) which is weakly convex in the other taxa such as *Neusticosaurus* (Sander 1989) and *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 14*a*, *c*). The upper jaw is matched by the straight dentary in *Serpianosaurus*, which again is slightly curved in the other taxa.

The skull of the Pachypleurosauridae shows negative allometric growth. This explains why the skull of *Pachypleurosaurus edwardsii* is relatively shorter than the skull of smaller genera such as *Neusticosaurus*. Adult specimens of *Serpianosaurus*, on the other hand, are as large or larger than adult *Neusticosaurus*, and yet their skulls are relatively longer than in the latter genus, justifying the use of relative skull length as a diagnostic feature of the first genus.

Morphology (figures 1 and 2)

The *premaxillae* are paired bones, covering the entire anterior part of the snout. Posterodorsally, the bone tapers to nasal processes that form most of the dorsal border of the external naris, entering between the nasal bones to a variable degree. The premaxilla meets the maxillary bone along the anterior margin of the external naris. In dorsal view the suture between premaxilla and maxilla trends in an anterolateral direction.

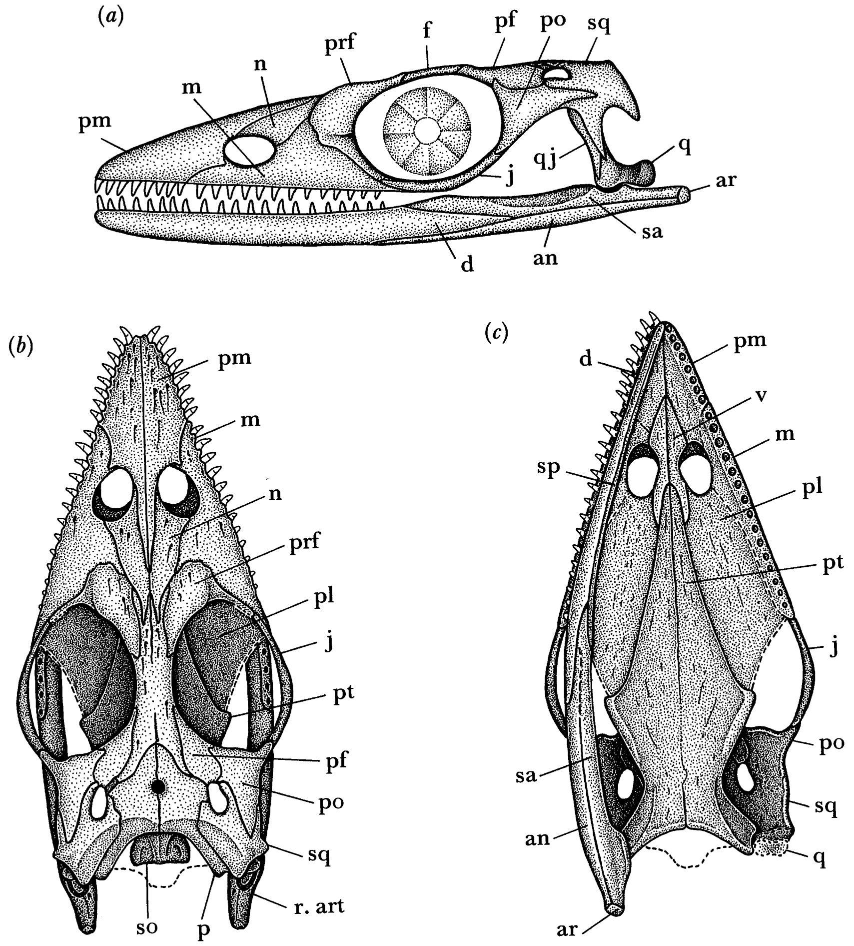

Figure 2. *Serpianosaurus mirigiolensis*, reconstruction of the skull in (*a*) left lateral view, (*b*) dorsal view and (*c*) ventral view. The left side of the skull table is reconstructed on the basis of specimen T 3686, the right side on specimen T 1071. The left side of the palate is reconstructed on the basis of specimen T 3689, the right side on specimen T 96.

The *maxillary* is a rather low and elongated bone; it forms the anteroventral, ventral and posteroventral margin of the external naris; the partly disarticulated specimen T 1071 shows the premaxilla to form a posterolateral projection anterodorsal to the external naris, which is received in a facet on the anterior portion of the maxilla. The nasal meets the ascending process of the maxilla behind the external naris. Posteroventrally, the maxilla forms a tapering process that underlies the contact of the anterior tip of the slender jugal with the posteroventral part of the prefrontal. Specimen T 1071 shows the anterior tip of the jugal to be embedded in a deep facet on the posteroventral part of the maxilla.

The *nasals* are paired bones; they typically participate in the formation of the posterodorsal margin of the external naris (T 951; T 1071; T 3771). In no specimen are the nasals fully separated from each other by a contact between premaxilla and frontals on the dorsal midline of the skull, as sometimes occurs in the genus *Neusticosaurus* (Kuhn-Schnyder 1974). However, the relation of these three bones is variable (figure 3). In T 951, the frontals form elongated anterior processes that enter deeply between the nasal bones, restricting the contact of the latter two elements with each other along the dorsal midline of the skull. In specimen T 3933 the elongated posterodorsal processes of the premaxillae enter deeply between the nasals, restricting the contact between the latter bones, but there is no unequivocal evidence that these premaxillary processes would have made contact with the anterior processes of the frontals. In T 3771, the nasals are in extensive contact with each other along the dorsal midline of the skull; posteriorly, they form an interdigitating suture with the frontals. The same situation obtains in the partly disarticulated specimen T 1071: in superficial view, the nasal forms the posterodorsal margin of the external naris, but deep to the posterodorsal (nasal) process of the premaxilla it extends anteriorly at least up to the level of the anterior margin of the external naris. The nasals meet along the dorsal midline of the skull behind the posterodorsal processes of the premaxillae and, even more posteriorly, they form an interdigitating suture with the frontals. In those specimens of *Neusticosaurus* that show a contact of the premaxilla and frontal, the two bones superficially overlap the dorsomedial contact between the two nasals. In *Pachypleurosaurus edwardsii*, the nasal bones are consistently separated along the dorsal midline of the skull by a contact of the frontals with the premaxillae.

The *frontal* bones are paired elements in T 951 and in T 3931. In all other specimens, the frontals show indications of fusion. In T 1071, the fusion of the two frontal bones is almost complete. This is not simply an expression of ontogenetic variation (late fusion of frontals during ontogeny) because the specimen T 3931 is one of the largest ones and still retains paired frontals. The frontal forms the rather straight dorsal margin of the orbit between the prefrontal and the postfrontal. Posterolaterally, the frontals form stout processes that extend between parietal and postfrontal; their exact length is sometimes difficult to determine because of crushing, but the specimens T 3680, T 3771 (right side of skull roof) and particularly T 1071 (right side of the skull table) clearly document the fact that the posterolateral processes of the frontals do not participate in the anteromedial margin of the upper temporal fossa.

The *parietal* bones are always paired in *Serpianosaurus*. They meet the posterolateral processes of the frontals in a suture that trends in an anteromedial direction. A fairly large pineal foramen is enclosed between the middle portions of the parietals. The posterior margin of the skull table is deeply embayed by the formation of posterolateral processes of the parietal that extend in a postero-ventro-lateral direction along the posteromedial processes of the squamosals (see below). The posterolateral processes of the parietals remain shorter than the squamosal bones, however. The contribution of the parietal and squamosal to the formation of the occiput is set off from the skull table by a ridge that marks the facet for the insertion of epaxial neck muscles.

The *prefrontal* is a curved element that forms the anterior and anterodorsal margin of the orbit. Its dorsal and dorsolateral portion is slightly expanded and therefore of an inflated appearance, whereas the ventral ramus (lateral foot-process), forming the anterior margin of

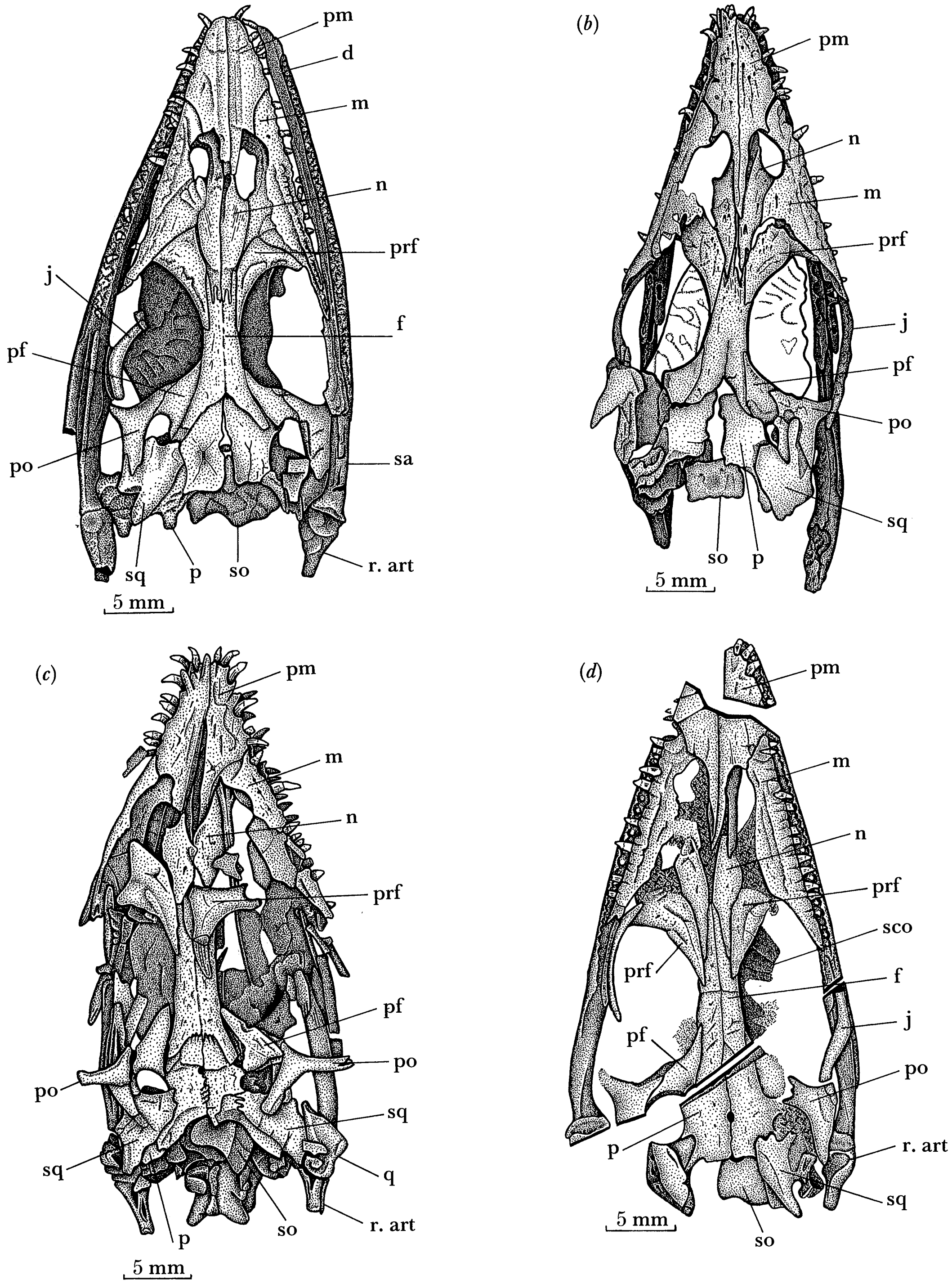

FIGURE 3. *Serpianosaurus mirigiolensis*, the skull in dorsal view. (*a*) Specimen T 3771; (*b*) specimen T 1071; (*c*) specimen T 3680; (*d*) specimen T 951.

the orbit as it curves down towards the palate is somewhat set off. No indication of a *lacrimal* bone is observed in any of the specimens, and T 1071 may be considered to be well-enough preserved to document its absence positively. Posterodorsally, the prefrontal forms a tapering process that is received in a facet on the surface of the frontal bone, as documented by specimen T 951. A contact of the prefrontal with the postfrontal is never established, a character that appears to be correlated with the relatively large orbits typical of pachyleurosaurids.

The relative size of the orbit is difficult to establish for *Serpianosaurus* because of the paucity of well preserved and undistorted specimens. In the well-preserved specimen T 3771 (figure 3*a*), the longitudinal diameter of the orbit equals 25.2% of the total skull length (as determined by the length of the lower jaw ramus (25.8% in specimen T 3684; 28.7% in T 951). Again in the well-preserved specimen T 3771, the longitudinal diameter of the orbit equals 54.3% of the length of the preorbital skull region (44.3% in T 3675; 53.3% in T 3684; 56.8% in T 951; 60% in T 3685).

The *postfrontal* is a rather broad element forming the dorsal part of the postorbital arcade. Along the posterodorsal margin of the orbit it forms a tapering anterodorsal process. It meets the ascending process of the postorbital in a somewhat sigmoidally curved suture that trends in a posteroventral direction. Dorsal to the postorbital, it forms the anterior and anterodorsal margin of the upper temporal fossa.

The *postorbital* appears as a triradiate bone in specimen T 3680 (figure 3*c*): the tapering ascending process rises up along the anterior margin of the postfrontal, thus forming the greater part of the posterior margin of the orbit. A rather short ventral process extends in an anteroventral direction, meeting the posterior tip of the jugal. The posterior ramus forms the anterior covering of the cheek region. It meets the platelike squamosal in a configuration that is difficult to establish. In specimen T 3680, the postorbital is a fairly slender bone, and preservation is such that the posterior ramus appears to overlap the platelike squamosal. In specimen T 3771 (figure 3*a*), however, the postorbital appears as a rather platelike bone; the posterior ramus forms the anterior and ventral covering of the cheek region, tapering to a blunt tip in its posteriormost portion. On both sides of the head, the posterior tip of the postorbital is observed to be embraced by the squamosal in a V-shaped suture, an observation that is corroborated by specimens T 1071 (right side of the head, dorsal view) and T 96, which shows the contact zone between postorbital and squamosal in ventral view. The interlocking of these two bones is best documented by the partly disarticulated skull table of specimen T 1071 (figure 3*b*, right side of the skull table). The postorbital forms a posterior ramus comparable to that observed in specimen T 3771, overlapping the rather plate-like squamosal. Superficially, the latter thus appears to embrace the posterior ramus of the postorbital with a distinct dorsal and a thinner as well as somewhat shorter ventral process. The overlap of these two bones lies further down on the cheek region (the ventral process of the squamosal appearing below the posterior ramus of the postorbital is thinner) than was described for the genera *Neusticosaurus* and *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 14).

A critical point is the participation of the postorbital in the margin of the upper temporal fossa in pachypleurosaurids (Schmidt 1987). The bone enters the relatively large upper temporal fossa in *Anarosaurus* (Carroll 1981), *Dactylosaurus* (Sues & Carroll 1985) and *Keichousaurus* (Young 1958). In *Pachypleurosaurus* and *Neusticosaurus*, the postorbital variably remains excluded from the anterior margin of the upper temporal fossa by a contact of the squamosal with the postfrontal, or enters it narrowly (Carroll & Gaskill 1985, p. 361). The

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situation is similar in *Serpianosaurus*. A contact of the postfrontal with the squamosal, excluding the postorbital from the temporal opening, appears to exist in the left side of the skull of specimen T 3680 (figure 3*c*); on the other hand, the postorbital appears to enter the anteroventral margin of the upper temporal fossa in specimen T 3771 (figure 3*a*). In the latter specimen, however, the anterior process of the squamosal, which lies between the lateral margin of the upper temporal fossa and the dorsal margin of the postorbital, seems to be broken, or it is variably developed. This at least is the conclusion reached on the basis of the comparison with specimen T 1071 (figure 3*b*), where the anterodorsal process of the squamosal participating in the interlocking suture with the postorbital is clearly demarcated. A facet can be observed in the surface of the postorbital that received the anterior tip of the squamosal process in the fully articulated skull, but the position of this facet leaves room for a very narrow participation of the postorbital in the anterior margin of the upper temporal fossa. This might have been the situation typical for *Serpianosaurus*, as is documented by the fragmentary skull table of specimen T 3685 (figure 4*a*). Here, the anterodorsal process of the squamosal comes very close to the postfrontal so that any contribution of the postorbital to the anterior margin of the upper temporal fossa must have been very narrow. In fact, exclusion from, or narrow participation of, the postorbital in the anterior margin of the upper temporal fossa may vary with the better or lesser development of the anterodorsal process of the squamosal.

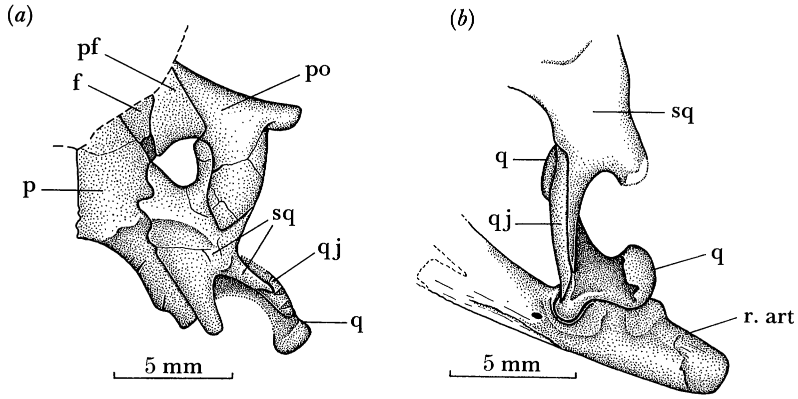

FIGURE 4. *Serpianosaurus mirigiolensis*, details of skull structure. (*a*) Right half of the skull table showing the bones surrounding the upper temporal fossa in specimen T 3685; (*b*) The quadrate and associated bones in specimen T 3678.

The upper temporal fossa of *Serpianosaurus* is small and of rounded or weakly triangular shape, somewhat as in *Pachypleurosaurus* (Carroll & Gaskill 1985). This is a marked contrast to *Neusticosaurus* where in one species the upper temporal fossa is narrow and slit-like or weakly keyhole-shaped, whereas it is oval in the other species (Sander 1989). The length of the upper temporal fossa amounts to 5.6% of the skull length (as determined by the lower jaw length) in the well-preserved specimen T 3771 (6.5% in specimen T 3709; 4.8% in specimen T 3685).

The ventral margin of the cheek region is emarginated as is visible in dorsal view, in contrast to *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985, p. 361).

The *squamosal* is restricted to a posterior position, embracing the posterior ramus of the postorbital; it is lined medially by the posterolateral process of the parietal. It forms the posterior and ventral margin of the upper temporal fossa, and the posterior part of the dorsal margin of the temporal embayment. The squamosal can be described as bearing four processes (figure 4*a*). The anterodorsal and anteroventral process embrace the posterior portion of the postorbital. The posteromedial process of the squamosal extends ventrally behind the quadrate; lined along its medial side by the posterolateral process of the parietal, it participates in the formation of the occiput. The posterolateral process of the squamosal overlaps the dorsal head of the quadrate in lateral view (specimen T 3685). It is better developed than was reconstructed for *Pachypleurosaurus* by Carroll & Gaskill (1985), which results in a more conspicuous notching of the squamosal dorsal to the quadrate suspension (see also specimen T 3771, left side of the skull).

The *jugal* is a curved and slender bone that approaches the prefrontal anteriorly and contacts the ventral tip of the postorbital posteriorly so as to complete the postorbital arcade. An actual contact of the anterior tip of the jugal with the lateral foot-process of the prefrontal, as is observed in *Neusticosaurus* and *Pachypleurosaurus*, is not documented for *Serpianosaurus*, although it seems likely to occur as judged from the facet on the right maxilla of specimen T 3680. Specimen T 3931 (right orbit), on the other hand, may be interpreted as showing a narrow separation of jugal and prefrontal by the intervening palatine bone which carries the infraorbital foramen for the passage of the maxillary division of the trigeminal nerve.

The presence of a *quadratojugal*, typical of *Nothosaurus* in general and of pachypleurosaurids in particular (Carroll & Gaskill 1985, p. 364), is well documented in specimen T 3678 (figure 4*b*). It is a narrow splint of bone applied to the lateral exposure of the quadrate, lying below and in front of the laterally descending posterior process of the squamosal (specimen T 3685).

The jaw suspension is well exposed in lateral view in specimen T 3678. The cephalic condyle of the quadrate has a narrow lateral exposure below the squamosal and in front of the quadratojugal. The narrow lateral edge of the shaft of the quadrate is covered anteriorly by the quadratojugal, posteriorly by the posterolateral process of the squamosal. The latter does not extend quite as far ventrally as does the quadratojugal; the ventral tip of the quadratojugal reaches the lateral exposure of the mandibular condyle of the quadrate. From below and behind the posterolaterally descending process of the squamosal emerges the quadrate conch. A peculiar feature, also reported for *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 14*f*), is the extension of the mandibular condyle into a posteriorly projecting head, which forms the base of the posterior quadrate notch and which must have been received in the deep facet lying just behind the mandibular articulation on the retroarticular process (the posterior projection of the mandibular condyle of the quadrate is also observed in the specimens T 3680 and T 3685). The quadrate notch of *Pachypleurosaurus* is believed to have supported a tympanum (Carroll & Gaskill 1985, p. 364).

The rectangular *supraoccipital* forms the posterior roof of the braincase; it typically projects beyond the posterior margin of the parietal skull table. In T 3771 the parietals have separated so as to disclose the ossified ascending process of the supraoccipital.

In none of the specimens investigated is the *palate* well preserved in its original position. The two better-preserved palates of the specimens T 96 and T 3681 will therefore be described in some detail (figure 5).

Both skulls are preserved in ventral view. The two halves of the palate have dissociated in their anterior parts in both specimens, which exposes the dorsal dermal covering of the facial portion of the skull in ventral view: in T 3681 it is possible to identify, from front to back, the

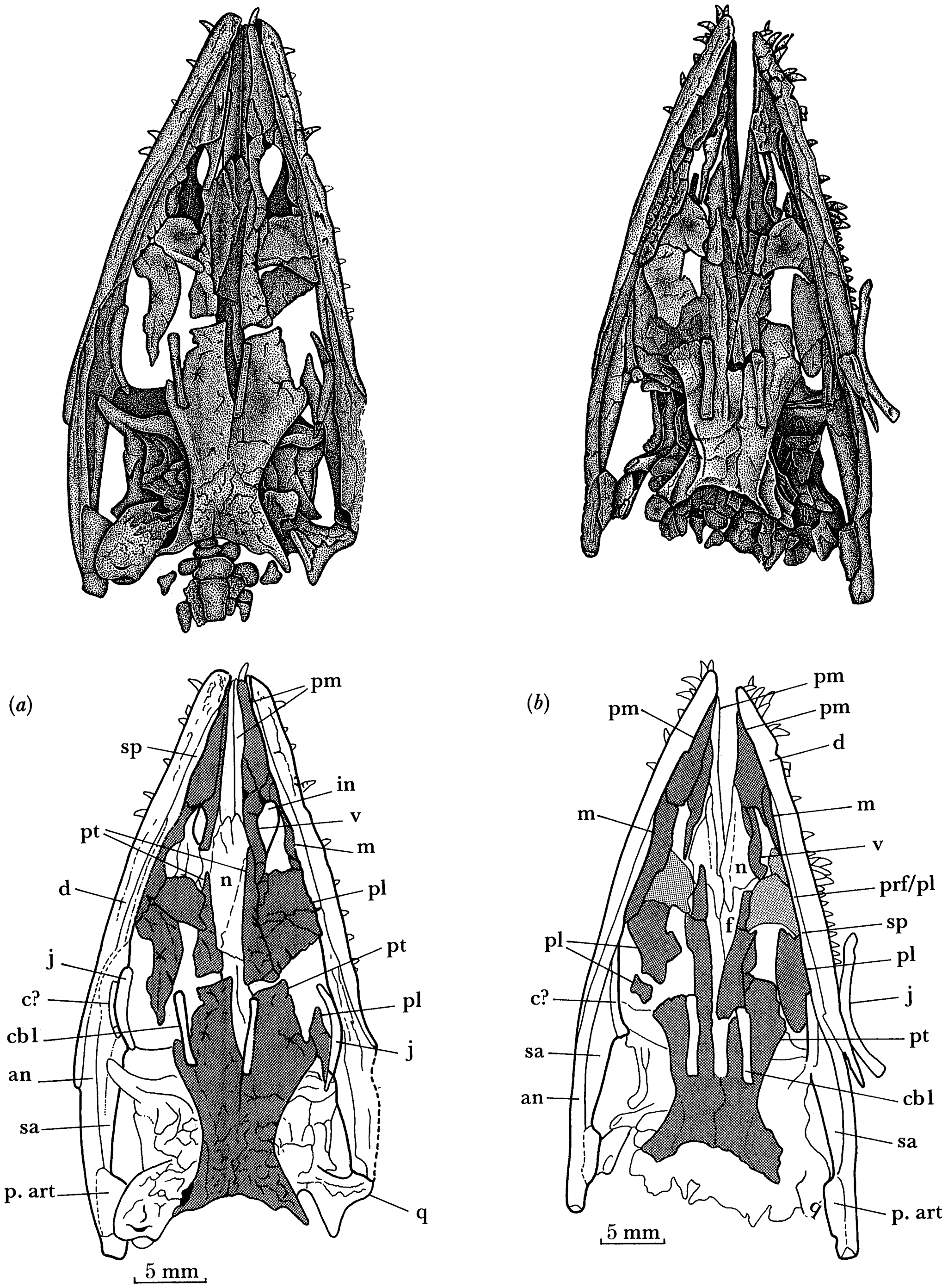

Figure 5. *Serpianosaurus mirigiolensis*, the skull in ventral view. The palatal bones are shaded in the keys to the specimen drawings. (*a*) Specimen T 96; (*b*) specimen T 3681.

dorsal (nasal) process of the premaxilla, the two nasal bones, and the ventral surface of the frontals.

Anterolaterally, the palatal surface is formed by palatal shelves of the *premaxilla* and of the maxilla; the two bones meet along the anterolateral margin of the elongated internal naris. Unlike *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985, fig. 14), the palatal shelf of the maxilla thus excludes the palatine bone from the lateral margin of the internal naris.

The medial margin of the internal naris is formed by the slender and elongate *vomer*. The vomers are paired elements and must originally have met along the ventral midline of the skull. Their anterior portion is triangular and extends anteriorly between the palatal shelves of the premaxillae, without reaching the anterior tip of the snout (T 96, figure 5*a*). The vomer meets the palatal shelf of the premaxilla along the anterior margin of the internal naris. Medial to the internal naris, the vomer forms a slender bar of bone that enters between palatine and pterygoid posteriorly, thereby excluding the latter bone from the margin of the internal naris. The *internal naris* is therefore enclosed by the premaxilla anteriorly and anterolaterally, by the maxilla posterolaterally, by the vomer anteromedially and medially, and by the palatine caudally. The exact shape of the posterior margin cannot be established.

The *pterygoid* bones meet along the ventral midline of the skull. Posteriorly they form a broad plate of bone, extending back to the occipital condyle, and thus covering all of the endochondral basicranium in ventral view. Posterolaterally, the pterygoid forms a broad process that meets the medial surface of the quadrate. The posterolateral process is set off from the palatal surface by a distinct and curved ridge, demarcating a facet that may have served as site of origin for the deep portion of the pterygoideus muscle. The posterolateral tip of the posterolateral process of the pterygoid forms a distinct spheno-occipital tubercle that must have served the tendinous insertion of part of the subvertebral (subaxial) cervical musculature.

At a level ventral to the orbit, both pterygoids are broken in an identical manner in both specimens. Behind this point they form a lateral extension that meets the palatine; anterior to these reduced transverse processes the pterygoid tapers, forming the palatine ramus which eventually establishes an overlapping contact with the vomer at the level of the posterior margin of the internal naris. This contact is particularly well preserved on the left side of the skull in specimen T 96 (figure 5*a*), documenting the fact that the pterygoid extended to a more anterior level compared with *Pachypleurosaurus edwardii* (Carroll & Gaskill 1985, fig. 14).

The *palatine* is a very thin plate of bone that is crushed over the underlying structures of the skull roof. On both sides of the skull of both specimens, the shape of the prefrontals is clearly identifiable, which renders it extremely difficult if not impossible to determine the configuration of the anterior end of the palatine bone.

The presence or absence of an *ectopterygoid* bone cannot be unequivocally established, because of crushing of the palatal bones. All that can be stated is that there is no unequivocal evidence of the presence of this element. The bone is most probably absent, because it is also not observed in any other of the well-preserved pachypleurosaur specimens from Monte San Giorgio.

As in other pachypleurosaurids, the subtemporal and inferior orbital fenestrae are confluent. This is a consequence of the reduction of the transverse process of the pterygoid and of the reduction or even loss of the ectopterygoid, so that the palate loses its contact with the ventral end of the postorbital arcade. The exact shape of the combined subtemporal and inferior orbital fossae is difficult to determine, however. On the right side of the palate of specimen T 3681 a sharp and sigmoidally curved edge of the palatine is observed to extend from the posterior tip of the palatal shelf of the maxilla in a posteromedial direction. The shape of the palatine bone then becomes obscured by underlying bone of uncertain identity, but in general the element seems to extend towards the reduced transverse process of the pterygoid. This configuration indicates the presence of a relatively large subtemporal fossa of roughly oval circumference, which becomes narrow at the level of the reduced transverse process of the pterygoid, merging into the inferior orbital fenestra which extends anteriorly as a slit-like opening up to the caudal tip of the palatal shelf of the maxilla. This interpretation of specimen T 3681 (figure 5*b*) is supported by examination of specimen T 96, and a similar configuration of the palate was tentatively restored for *Pachypleurosaurus edwardsii* by Carroll & Gaskill (1985, fig. 14).

The *lower jaw* is preserved in ventral view in the specimens T 96 and T 3681 (figure 5). Because of crushing and consequent dissociation of the elements, both specimens clearly display the posterior extent of the *dentary* bone up to a level shortly behind the low coronoid process. The ventral and lateral surface of the posterior part of the lower jaw ramus is covered by the *angular* bone, which extends anteriorly along the ventromedial edge up to a level ventral to the orbit, as is well documented by specimen T 96. The anterior tip of the angular is overlapped by the *splenial* which completes the ventromedial edge of the lower jaw up to a level closely behind the jaw symphysis. In ventral view, the *articular* bone caps the posterior tip of the retroarticular process. The *prearticular* flange, which underlies the mandibular joint, is broken on both sides of the skull in specimen T 3681. The adductor fossa is bordered laterally by the *surangular*, the dorsal margin of which gently rises up to the tip of the coronoid process. A slender *coronoid* bone can be identified running from the apex of the low coronoid process in an anterior direction along the dorsomedial margin of the lower jaw ramus of specimen T 3681; in specimen T 96, the identification of the coronoid bone is rendered difficult by the impressions of the underlying jugal bone.

Dentition

The teeth of *Serpianosaurus* share the thecodont implantation typical of pachypleurosaurids and indeed of nothosaurs in general. The anterior teeth on the premaxilla and on the dentary are long and distinctly recurved. Most posterior teeth on the premaxilla and on the dentary, like those on the maxilla, are somewhat shorter, and a slightly expanded but monocuspid crown can be distinguished from the weakly striated base.

There are six to eight functional tooth positions on the premaxilla (specimen T 1017: six or seven tooth positions in the right premaxilla; T 3679: eight tooth positions on both premaxillaries; T 3680: seven tooth positions on the right premaxilla, six or seven on the left; T 3931: six or seven tooth positions on the right premaxilla, eight tooth positions on the left; T 3933: six tooth positions on the left premaxilla). The premaxillary tooth count is thus comparable to that of *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985, p. 364). On the maxilla, however, the latter genus appears to bear more teeth (14 plus 5; Carroll & Gaskill 1985, p. 364) than *Serpianosaurus*: the best-preserved specimen T 3931 shows 15 (left) to 16 (right) tooth positions on the maxillae with apparently nearly alternate tooth replacement on the posterior part of the bone. T 951 shows approximately 15 tooth positions on the left maxilla.

The teeth on the dentary are best preserved in specimen T 3931. A minimum of 31 tooth positions are counted on the left dentary and 32 tooth positions on the right. The exact number of teeth is difficult to establish because of tooth replacement. But if the tooth counts given above are correct, it would mean that the spacing of the teeth varies from front to back along the lower jaw ramus. The left dentary in particular shows a distinctly closer spacing of the teeth towards the middle portion compared with the anterior or posterior parts of the bone. The teeth on the dentary are clearly more numerous than on the upper jaw; accordingly, the dentary tooth row extends further back than the maxillary tooth row, up into the anterior portion of the suborbital vacuity, as is shown by specimen T 1071. The function of these posterior dentary teeth remains unknown.

The entire palatal surface of *Serpianosaurus* is devoid of dentition.

Compared with *Neusticosaurus* (5 teeth on the premaxilla, 12 or 13 on the maxilla and 25 on the lower jaw) it can be stated that *Serpianosaurus* bears more teeth both in the upper and lower jaw (Sander 1989).

The axial skeleton

Vertebral column

The vertebrae of *Serpianosaurus* are amphicoelous (platycoelous) throughout the length of the vertebral columm, as is also observed in other pachypleurosaurids. Carroll & Gaskill (1985, p. 366) note that the presence of a neurocentral suture is a common feature of aquatic forms: they are observed throughout the vertebral column in *Serpianosaurus*. Specimen T 3933 (figure 6*a*) shows cervical vertebrae preserved in lateral view displaying neurocentral sutures with no separation between the elements, however. The same is true for laterally exposed dorsal vertebrae in specimen T 3931, where some slippage has occurred between centrum and neural arch in spite of the large size of the individual. T 1045 is the second-largest specimen included in the study, and it shows clear dissociation of centrum and neural arch in several caudal vertebrae.

With a count of 35–38, the number of presacral vertebrae in *Serpianosaurus* falls into the range of variability of the geologically younger species of *Neusticosaurus* and of *Pachypleurosaurus edwardsii*. The number of sacral vertebrae varies between three and four in *Serpianosaurus*. The number of caudal vertebrae is difficult to determine because the tip of the tail is missing in most specimens; T 3681 shows a complete tail including 58 vertebrae. T 96 is another specimen with a complete tail, but the last sacral vertebra is less clearly identifiable: as far as can be determined, the tail includes 52 vertebrae. T 3931 with a well-preserved but slightly disarticulated tail shows a minimum of 47 caudal vertebrae.

The older literature on pachypleurosaurid systematics stresses the length of the neck relative to that of the trunk (determined by the number of cervical versus dorsal vertebrae) as an important taxonomic character. Unfortunately, the demarcation of cervical from dorsal vertebrae is a matter of definition in reptiles (Hoffstetter & Gasc 1969), and it is difficult in fossils where the transition between the two zones is often obscured by overlapping elements of the pectoral girdle. If all those vertebrae that lie in front of the clavicles are interpreted as cervicals, one obtains 15–18 cervicals (14? in specimen T 3406) as opposed to 20–23 dorsal vertebrae. Zangerl (1935) and Carroll & Gaskill (1985, p. 367) identified the division between the cervical and trunk vertebrae in *Pachypleurosaurus* by a shift in rib articulation: whereas the ribs of the neck are double headed, articulating with the neural arch (tuberculum) and centrum (parapophysis) (figure 6*a*), those of the trunk are single headed and have lost all connection to the centrum. Although the same general situation obtains in *Serpianosaurus*, the transition from double-headed to single-headed ribs is not really abrupt (posterior cervical or anterior dorsal ribs tend to develop a broad proximal head or synapophysis (Hoffstetter & Gasc 1969, p. 252)). The situation is further obscured by the fact that most specimens preserve the cervical vertebral columns in dorsal view, so that the broad and fluted postzygapophyses conceal the proximal rib articulations. However, specimen T 3406 shows double-headed (dichocephalous) ribs in front of the clavicles and interclavicle, and single-headed (holocephalous) ribs behind these elements. In specimen T 3931, the transition from dichocephalous to holocephalous ribs is likewise observed close to the (disarticulated) clavicles, thus corroborating the counts of cervical vertebrae indicated above.

The atlas–axis complex is difficult to describe in detail. In most instances the atlas is crushed, as is the occiput of the skull, or the anteriormost cervical vertebra is at least partly covered by the dislocated supraoccipital.

In most reptiles, the axis is distinctly larger than the atlas and, to a lesser degree, than the succeeding third cervical vertebra. This may be so on account of the head extensors, of which many originate from the axis neural arch (Oelrich 1956; Tschanz 1986). Although this pattern was not observed in *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1986, p. 367), the axis can be distinguished by its size in *Serpianosaurus*. In specimen T 951, the axis measures 4.4 mm in dorsal view, whereas the succeeding third cervical vertebra measures 3.1 mm across the neural spine. Specimen T 96 displays the atlas–axis complex in ventral view. The atlas centrum is approximately 1.6 mm long, the axis centrum measures 3.0 mm.

The atlas–axis complex in specimen T 96 shows considerable anatomical detail (figure 5*a*). The atlas centrum is nearly circular or oval in ventral view. Two atlas ribs are identifiable. The presence of atlas ribs is also documented in specimen T 3677. No intercentrum 2 is observed between atlas and axis, in contrast to *Neusticosaurus*. A bony element in front of the atlas might be interpreted if not as a displaced intercentrum 2, then as intercentrum 1, a bone that is possibly also present in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 368) but not in *Neusticosaurus*. The paired atlas neural arches are disarticulated and well exposed in specimen T 3931. They correspond to the primitive reptilian condition (Romer 1956, p. 234). Each atlas arch has a triradiate appearance. The rather broad dorsal process participated in the formation of a distinct neural spine. Posteriorly, the atlas arch bears a slender postzygapophyseal process articulating with the axis. The ventral process established contact with the atlas centrum.

The other cervical vertebrae gradually increase in size from front to back: they become both longer and broader in dorsal view, as is particularly well exemplified by the undistorted specimen T 1071. The third cervical vertebra is approximately 2.9 mm long (measured across the neural spine) and 4.9 mm broad (measured across the postzygapophyses). The 18th vertebra (last cervical) is 3.9 mm long and 7.3 mm broad. The width of the vertebrae increases by a widening and 'inflation' (pachyostosis, figure 6*b*) of the postzygapophyses. The neural spines remain low throughout the cervical region, represented by little more than a longitudinal ridge on the dorsal surface of the neural arch. Specimen T 3933 shows the cervical region of the vertebral column well preserved in lateral view. The suture between neutral arch and centrum is irregularly V-shaped. The tuberculum of the rib articulates with the diapophysis formed jointly by the neural arch and the centrum; as a consequence, the neurocentral suture passes right through it (figure 6*a*). A short transverse process of the centrum forms a concave facet that receives the tuberculum; the neural arch forms a dorsal buttress to this facet. It appears that the neural arch contribution to the formation of the diapophysis becomes progressively reduced from front to back, but twisting of the cervical vertebral column in the critical region precludes a definitive statement. The parapophysis (articulating with the capitulum) lies just posteroventral to the diapophysis, close to the ventral edge of the centrum. The articular processes of the cervical vertebrae become progressively more prominent from front to back along the vertebral column.

The trunk vertebrae retain the general shape of the posterior cervical vertebrae. As the ribs

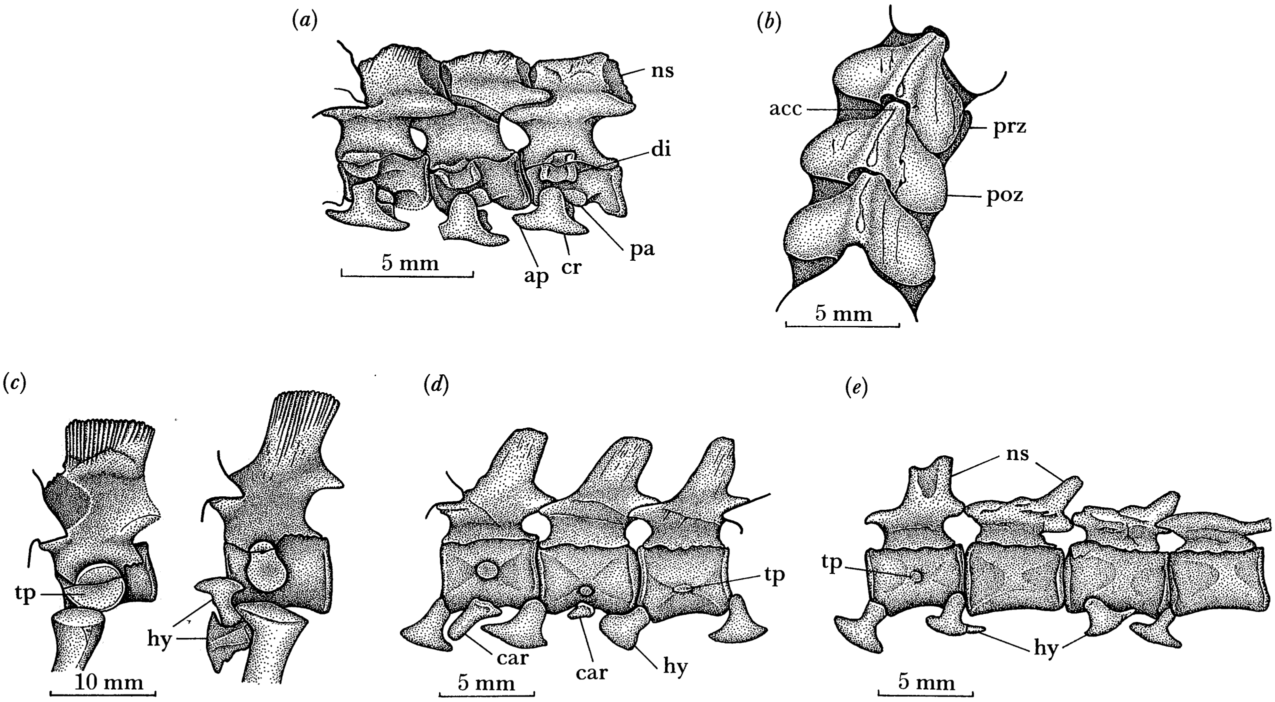

FIGURE 6. *Serpianosaurus mirigiolensis*, vertebral column. (*a*) Specimen T 3933, cervical vertebrae 3, 4 and 5 in left lateral view; (*b*) specimen T 1071, cervical vertebrae 11, 12 and 13 in dorsal view; (*c*) specimen T 1045, caudal vertebrae 1 and 4 in left lateral view; (*d*) specimen T 3933, caudal vertebrae 10, 11 and 12 in left lateral view; (*e*) specimen T 3933, caudal vertebrae 14, 15, 16 and 17 in left lateral view.

become holocephalous, however, the parapophysis is lost on the centrum, whereas the diapophysis on the neural arch is distinctly enlarged, shifted to the anterior portion of the trunk vertebra, at least in the middle and posterior part of the trunk (specimen T 3931), where it forms a distinct transverse process. Specimens preserved in ventral view show a smoothly rounded ventral surface of the centrum. The relatively undistorted specimen T 1071 shows that the size of the vertebrae of the trunk region does not vary greatly in dorsal view. More posterior dorsal vertebrae are slightly broader across the 'inflated' (pachyostotic) postzygapophyses than the anterior vertebrae. What does vary, however, is the size of the neural spine which increases in height from front to back. In the well-preserved specimen T 1071, the neural spine remains a low dorsal ridge with an intact dorsal edge up to the 32nd vertebra (14th dorsal). The height of this dorsal ridge increases very slightly within the dorsal region. Most posterior vertebrae, however, show a broken surface of the neural spine, indicating an increase in height. The increasing height of the neural spines is also documented by a frequently observed rotation within the vertebral column of the dorsal region. In the well-preserved specimen T 3931, for example, the vertebrae are preserved in dorsal view and retain an intact neural ridge up to the 24th element (9th dorsal vertebra). The 25th through to the 33rd vertebrae tend to tilt to a lateral position, and the surface of their neural spine is broken, indicating an increase in height. From the 34th element on through the tail, the vertebrae are preserved in a lateral position, showing an increasing height of the neural spine up to the base of the tail. In the posterior dorsal, sacral, and caudal regions the height of the neural spines has caused the vertebrae to tilt to a fully lateral position during the embedding of the fossil. A similar situation also obtains in *Pachypleurosaurus edwardsii*, where the increase in height of the neural spines starts already in the posterior cervical and anterior dorsal region, however (Carroll & Gaskill 1985).

The number of sacral vertebrae varies between three and four in *Serpianosaurus*. Carroll & Gaskill (1985, p. 371) note that only three sacral vertebrae can unequivocally be identified in *Pachypleurosaurus*. Three sacral vertebrae is the more frequently observed condition in *Serpianosaurus* (see below and figure 10*a*). However, the ribs of the following (1st caudal?) vertebra are curved in an anterior direction, as is also the case in *Pachypleurosaurus*, and sometimes they come into contact with the posteriormost tip of the ilium, so becoming a fourth sacral vertebra (see below and figure 10*b*). The sacral ribs are not ankylosed to the sacral vertebrae, and they show a broad proximal head, often retaining indications of the dichocephalous condition (specimen T 3931). As in *Pachypleurosaurus* (Carroll & Gaskill 1985, pp. 369–370) the sacral vertebrae differ from the trunk vertebrae by their extensive transverse processes, which are formed by the neural arch as well as by the centrum. The neurocentral suture is well exposed, passing through the transverse process in specimen T 1045. In this feature, the sacral vertebrae correspond to the anteriormost caudal vertebrae. Specimen T 3931 shows that these transverse processes increase in width from the 1st to the 3rd sacral vertebra, in correlation with the size of the proximal head of the sacral ribs. The neural spines of the sacral vertebrae continue the trend of an increasing height which begins within the dorsal region of the vertebral column.

The swollen (pachyostotic) appearance of the trunk vertebrae as seen in dorsal view is less pronounced in the sacral region, and vanishes within the anterior caudal region. The anterior caudal vertebrae bear transverse processes for the articulation of the caudal ribs. These processes diminish in size from front to back, and although the neural arch continues to contribute to their formation immediately behind the sacrum, the transverse processes progressively shift down on to the centrum more posteriorly. In specimen T 3931 (four sacral vertebrae) the 3rd caudal vertebra is the last one that receives a contribution from the neural arch in the formation of its transverse process. In specimen T 1045 (with three sacral vertebrae) the 4th sacral vertebra is the last one to show a contribution of the neural arch to the formation of the transverse process; in specimen T 3933 (three sacral vertebrae), the corresponding vertebra is the 6th caudal element. The same situation obtains in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 370), and as the latter genus, there is some variation as to the position of the last caudal vertebra bearing a transverse process. As the reduction is gradual, it is often difficult to determine which vertebra is to be considered the last one to bear a rudiment of the transverse process. The range of variability extends from the 11th (12th) caudal vertebra in specimen T 3676 with three sacral vertebrae (12th caudal vertebra in specimen T 3931 with four sacral vertebrae) to the 14th (15th) caudal vertebra in specimen T 3933 with three sacral vertebrae (14th caudal vertebra in specimen T 3677 with four sacral vertebrae). It is questionable whether caudal ribs are attached to the posteriormost rudiments of transverse processes in all specimens (see below).

The neural spines of the caudal vertebrae initially increase in height and thus continue the trend initiated in the posterior dorsal and sacral region. The tallest neural spines throughout the vertebral column are observed on the first three to five caudal vertebrae (figure 6*c*). More posteriorly, the neural spines decrease in size again (figure 6*d*). Within the tail, the neural spines show a progressively increasing posterodorsal inclination, and there is a rather abrupt transition from a small but still conspicuous neural spine to a neural arch forming but a longitudinal ridge on the vertebrae. In specimen T 3931, this transition occurs between the 15th and 16th caudal vertebra, in the well-preserved tail of the specimen T 3933 the transition lies between the 16th and 17th caudal vertebrae (figure 6*e*), in specimen T 3676 it lies between the 14th and 15th caudal vertebrae. All other specimens with a well-enough preserved tail fall into this range of variability.

The haemal arches are comparable in size, shape and position to those of *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985). They are in a primitive intervertebral position, and diminish in size from front to back. Anteriorly, they form a vertical pedicel bearing a distinct distal expansion (figure 6*c*). More posteriorly, they assume an anchor-like appearance, with a short pedicel bearing a curved anterior and posterior projection distally (figure 6*d*, *e*). The posteriormost haemal arches have a very short pedicel, so that the curved anterior and posterior projections come to underlie the intervertebral joint. Carroll & Gaskill (1985, p. 370) note that haemal arches may be missing in the anteriormost part of the tail of *Pachypleurosaurus*; a similar situation obtains in *Serpianosaurus*, although the preservational condition of the specimens does not allow an accurate assessment of numbers. Nevertheless, there is no specimen that shows remains of haemal arches lying in front of the 3rd or 4th caudal vertebrae. On the other hand, haemal arches do not extend up to the tip of the tail. Well-preserved specimens (T 96, T 3676, T 3677, T 3933) show that the last haemal spine was between the 28th and 29th, and 30th and 31st, caudal vertebrae respectively. A point difficult to explain is the total absence of haemapophyses in the otherwise well-preserved specimens T 1071 and T 3931.

The increased height of the neural spine in the anterior third of the tail, together with the haemal arches, results in the formation of a dorsoventrally extended surface which served a propulsive function during aquatic locomotion. Also of particular interest with respect to aquatic locomotion are additional intervertebral articulations typical for pachypleurosaurids in general and described in detail for *Pachypleurosaurus edwardsii* by Carroll & Gaskill (1985, p. 369): 'nearly all of the vertebrae in the neck region, trunk and anterior portion of the tail have the anterior margin of the base of the neural spine fitting into the posterior margin of the more anterior vertebrae between the zygapophyses'. Kuhn-Schnyder (1959, p. 643) identified these articulations as a zygosphene–zygantrum system. Hoffstetter & Gasc (1969, p. 250) have given an explicit definition of the zygosphene–zygantrum system that does not match the condition observed in several squamates, nor that of aquatic eosuchians (Currie 1981, 1982) or of pachypleurosaurids. It therefore seems more appropriate to keep a description in more general terms. The well-preserved specimen T 1071 shows an unpaired anterior and medial projection from the base of the neural arch articulating with a facet situated between the postzygapophyses of the preceding vertebral element (figure 6*b*). This articulation is observed in *Pachypleurosaurus edwardsii* all along the cervical, dorsal and anterior caudal region of the vertebral column (Carroll & Gaskill 1985, p. 369). Kuhn-Schnyder (1959, p. 643) mentions a similar condition in the pachypleurosaurids from Monte San Giorgio in general, as well as in a specimen from the Stulseralp (Kanton Graubünden). As exposed in dorsal view, these accessory articulations are most prominently developed in the cervical region of *Serpianosaurus* (specimen T 1071 (figure 6*b*)), and they persist in the anterior dorsal region, but seem to disappear more posteriorly. Partial separation of posterior dorsal and anterior caudal vertebrae in the specimens T 951 and T 1071 shows, however, a median projection from the neural arch still being present in the posterior dorsal and anterior caudal region, although they have shifted to a somewhat deeper level, and thus tend to be obscured in the dorsal view of fully articulated vertebrae. The accessory articulations are also prominently developed between the sacral vertebrae.

Carroll & Gaskill (1985, p. 369) describe additional and deeper accessory articulations between the posterior trunk vertebrae consisting of 'paired processes extending posteriorly below the level of the zygapophyses of the posterior trunk vertebrae, so as to fit between the bases of the anterior zygapophyses of the next vertebra'. These processes are visible on the disarticulated posterior dorsal vertebrae of specimen T 3935 (Carroll & Gaskill 1985, fig. 2). Separate paired posterior processes were not observed on the posterior dorsal vertebrae of *Serpianosaurus*. The only specimen to document a double intervertebral articulation between the partly disarticulated last dorsal and first sacral vertebrae is T 1071. The anterior dorsomedial process of the posterior (first sacral) vertebra fits into a groove between the postzygapophyses of the preceding (last dorsal) vertebra as described above; from below this groove emerges a posterior median and ventral projection that fits into a groove on the anterior aspect of the first sacral vertebra, lying between its prezygapophyses but below the anterior dorsomedial projection. This posterior projection on the last dorsal vertebra is of a broad triangular shape subdivided by a longitudinal ridge, and terminates posteriorly in a slightly bifurcated tip. This indicates a paired origin of the posterior projection: it seems to have arisen by fusion of the paired processes described by Carroll & Gaskill (1985).

The nearly three-dimensionally preserved specimen T 1071 shows the prezagypophyses to appear like a deep groove in lateral view, into which fit the postzygapophyses of the preceding vertebra. The articulation of the vertebrae lies in a transverse plane. This arrangement restricts lateral bending of the vertebral column, as mentioned by Sues & Carroll (1985, p. 1603) with respect to *Dactylosaurus*.

Ribs

As stated previously, ribs extend throughout the cervical, dorsal and anterior caudal region of the vertebral column. Atlas ribs are present on specimens T 96 and T 3677. Throughout the cervical region and into the anterior dorsal region the ribs increase in length and curvature. In the middle part of the trunk, the ribs are of nearly constant size, whereas the last three (specimen T 3931) to five (specimen T 1071) dorsal ribs decrease in size again as they approach the sacrum, forming loosely defined 'lumbar ribs'. True 'lumbar vertebrae' defined by Hofstetter & Gasc (1969, p. 203) on the absence of ribs or on the presence of fused ribs, are lacking in *Serpianosaurus* because unfused ribs extend throughout the trunk region. As noted above, the cervical ribs are dichocephalous, whereas those of the trunk are holocephalous, with one or two ribs of the pectoral area representing intermediate stages.

A remarkable feature of *Serpianosaurus* is the presence of an anterior process on the cervical ribs. As documented by specimen T 3933 (figure 6*a*), the broad tuberculum is received in a facet (diapophysis) formed jointly by the neural arch and centrum. Deep and somewhat below the tuberculum lies the capitulum, which articulates with the centrum ventral and slightly posterior to the diapophysis. In addition to these two articular heads the cervical ribs form an anterior process throughout the cervical column. The anterior process is long enough to bridge the intervertebral joint. The position of tuberculum and capitulum with respect to each other and to the vertebral element is shown in dorsal view in specimen T 3931 (7th cervical vertebra), with the capitulum lying deep to the tuberculum, and articulating with the vertebral centrum slightly posteroventral to the tuberculum articulation. The absence of an articulation of the anterior process with the cervical vertebrae is shown in dorsal view by specimen T 96: the anterior process of the cervical ribs lies lateral to the vertebral element.

The sacral ribs are not ankylosed to the sacral vertebrae; they are dissociated from the respective vertebra in most fossils. Specimen T 3931 shows particularly well that the length of the sacral ribs decreases from front to back within the sacrum, whereas the distal and proximal expansion of the sacral ribs increases in the same direction. The shape of the expanded proximal head of the sacral ribs recalls the dichocephalous condition. Distally, three sacral ribs converge upon the medial side of the reduced dorsal process of the ilium. As in *Pachypleurosaurus*, three sacral ribs is the typical number. However, the first, and sometimes even the second (specimen T 3931) and third, caudal ribs are curved in an anterior direction, and the first 'caudal' rib may thus come to support the caudal surface of the dorsal process of the ilium (see below, figure 10). If this situation obtains, as in specimen T 3931, there are four sacral vertebrae and ribs.

The caudal ribs diminish quickly in size from front to back, and it is not clear whether they extend as far posteriorly within the tail as do the rudiments of the transverse processes. Specimen T 3931 is the only one among all those examined that shows caudal ribs in proximity to the 12th caudal vertebra, the last one to bear rudiments of transverse processes. On the other hand, specimen T 3933 shows a tail well preserved in lateral view. Rudiments of transverse processes extend up to the 14th (15th) caudal vertebra, but the last caudal rib is associated with the 11th caudal vertebra, and it is reduced to such a small size as to make it unlikely that further caudal ribs would follow (figure 6*d*, *e*). A similar situation obtains in specimen T 3681, where the 13th (14th) caudal vertebra is the last one to bear rudiments of transverse processes, whereas the last caudal rib is associated with the 10th caudal vertebra.

The ribs of *Phygosaurus* (Strasbourg specimen) have been described as providing two diagnostic features of the genus. Peyer (1934) noted that the ribs of *Phygosaurus* are oblong in cross section near their proximal end; Zangerl (1935) has pointed out, however, that a similar outline of the proximal cross section is observed in the geologically youngest pachypleurosaurids from Monte San Giorgio, coming from Alla Cascina. The latter correspond to *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985, p. 355).

On the other hand, Carroll & Gaskill (1985, p. 349) stress that the ribs and vertebrae of the Strasbourg specimen 'especially well seen in X-ray (Peyer 1933 [should read 1934]), do not exhibit pachyostosis, which is particularly well pronounced in the larger specimens in the Zürich collection'. This peculiarity of *Serpianosaurus*, shared with *Phygosaurus*, is well corroborated by the relatively large specimens T 1045 (glenoid–acetabulum length *ca.* 187 mm) and T 3931 (glenoid–acetabulum length 148 mm) from Monte San Giorgio. A specimen of intermediate size, T 3406 with a glenoid–acetabulum length of *ca.* 101 mm, shows likewise the total absence of pachyostosis. Smaller specimens, however, such as T 1071 (glenoid–acetabulum length *ca.* 77 mm), T 3933 (glenoid–acetabulum length *ca.* 92.5 mm) show slight pachyostosis, especially in the proximal segments of the ribs. The smallest specimen investigated, T 132 with a glenoid–acetabulum length of 41 mm, shows delicate ribs again. Pachyostosis, although always only very weakly expressed, may thus vary during ontogeny, although no consistent pattern can be discerned.

Gastral ribs

Another important feature, considered to diagnose the genus *Phygosaurus* in the older literature, relates to the structure of the gastral ribs as described for the Strasbourg specimen. Deecke (1886) described the Strasbourg specimen as showing gastral ribs that correspond in structure to those of other pachypleurosaurids: there is a broad ventromedial element, bearing an anterior projection, and a slender, spindle-shaped lateral element on either side of it. Deecke's description was criticized by Döderlein (in Steinmann & Döderlein 1890, fig. 770), who noticed two lateral elements on either side of each unpaired medioventral bar, except perhaps in the most anterior region of the trunk. The more medial one of these lateral elements is spindle-shaped, whereas the most lateral element is expanded laterally. Arthaber (1924, p. 495) quoted Döderlein's observations, which were also corroborated by Peyer (1934, p. 102) and Zangerl (1935, p. 68); the latter author quotes a personal communication of B. Peyer, who observed a similar construction of gastral ribs, each consisting of a total of five elements, in *Anarosaurus*.

The specimens of *Serpianosaurus* from the Monte San Giorgio correspond to the description of the Strasbourg specimen with respect to the gastral ribs. In none of the specimens bearing data on stratigraphy and locality is it possible to observe a complete gastral rib *in situ*, however. Yet the specimens T 3681, T 3931 and particularly the specimens T 1045, T 3678 and T 3679 with a disarticulated gastral rib cage permit the reconstruction of the composition of the gastral ribs at least for the middle and posterior part of the trunk (figure 7*a*, *b*). The most conspicuous element is the medioventral one, broad in its middle portion, but tapering laterally. The middle portion bears a blunt anteromedial projection, and it is angulated, enclosing an angle of approximately 120°. In *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 16*f*) and *Neusticosaurus* the angle enclosed by the two shanks of the medioventral gastral element increases from front to back; the same situation is observed in *Serpianosaurus*: in specimen T 3676 the medioventral element encloses an angle of approximately 95° anteriorly and 140° posteriorly. The width of the medioventral element measures 37 mm in the posterior trunk region of T 1045. The medioventral element shows an overlapping articulation with a slender and spindle-shaped element of 20 mm length on either side (T 1045, posterior trunk region). Laterally, the gastral rib cage is completed by slender bars of bone approximately 16 mm long (T 1045, posterior trunk region), showing a somewhat broadened, flattened and curved lateral portion, originally extending in a dorsal direction to complete the rib cage formed by the dorsal ribs. Döderlein (quoted by Arthaber (1924)) felt uncertain about the composition of gastral ribs in the anterior trunk region. There is some indication in the Monte San Giorgio specimens that gastral ribs may be composed of three elements only – the medioventral one and a lateral one on each side – in the anterior trunk region. In specimen T 3680 the most anterior lateral element that is observed, with a somewhat broadened and curved distal end, articulates with the anterior margin of the medioventral element lateral to the 25th presacral vertebra. This observation is contradicted, however, by specimen T 3676 which shows each gastral rib to be composed of five elements even in the 3rd gastral rib.

The mode of articulation of the five elements in *Phygosaurus* has been schematically figured by Döderlein in Steinmann & Döderlein (1980, fig. 770) and was corroborated by Peyer (1934, plate 39). The spindle-shaped element lies along the anterior margin of the lateral shank of the medioventral element; the most lateral element in turn lies along the anterior margin of the

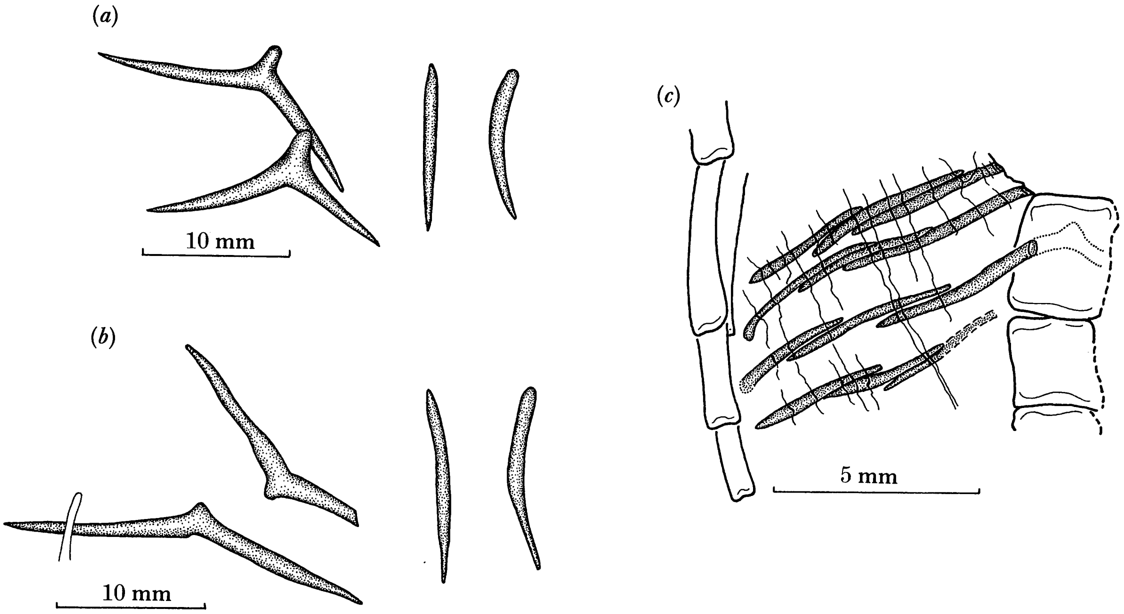

FIGURE 7. *Serpianosaurus mirigiolensis*, gastral ribs. (*a*) Specimen T 3679, anterior dorsal region; from left to right the medioventral, the intermediate and the lateral element. (*b*) Specimen T 3679, posterior dorsal region; from left to right the medioventral, the intermediate and the lateral element. (*c*) Specimen T 3391 (fragmentary); gastral ribs *in situ*, ventral view.

lateral portion of the spindle-shaped element. This reconstruction is corroborated by specimen T 3391 from Monte San Giorgio (figure 7*c*), which is problematical, however, because of the lack of any data concerning the locality and age of collection. The specimen consists of the most posterior trunk region, involving the last four dorsal vertebrae, the sacrum and the hind limbs, as well as the base of the tail. It is at the lower size range of *Serpianosaurus*, but with the femur measuring 13.7 mm, it is larger than the smallest *Serpianosaurus*, T 132. The femur length:standard length ratio is approximately 1.18, a value that falls into the range of variability of *Serpianosaurus*. Specimen T 3391 shows the gastral ribs *in situ*, with the five elements articulating in the manner reconstructed by Döderlein.

Deecke (1886, p. 176) counted two gastral ribs per vertebral segment in the Strasbourg specimen, an observation corroborated for *Serpianosaurus* by the problematical specimen T 3391, at least as far as the posterior trunk region is concerned. In none of the specimens from the Monte San Giorgio bearing exact data on locality and geological age could the number of gastral ribs per vertebral segment be determined unequivocally, but specimen T 1045 shows that gastral ribs clearly outnumber vertebrae and dorsal ribs at least in the posterior trunk region, whereas in specimen T 3931 two medioventral elements of gastral ribs emerge from below of each of the dorsal vertebrae numbered 17–19. A similar result obtains in the posterior trunk region of specimen T 3676. A well-preserved gastral rib cage of *Neusticosaurus* documents the occurrence of two gastral ribs per vertebral segment in this genus.

The appendicular skeleton

Pectoral girdle

The pectoral girdle of *Serpianosaurus* (figure 8) is composed of the interclavicle, clavicles, scapular blades and coracoids.

The interclavicle combines with the clavicles to form a solid and more or less straight transverse bar that, as mentioned above, lies behind the 15th–18th presacral vertebrae. It is of much narrower construction than the comparable portion of the pectoral girdle in *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 16). Partial or total disarticulation of the components is the usual condition observed in *Serpianosaurus*, which might indicate a somewhat looser connection between the bones than is typical for *Pachypleurosaurus*. As in the latter genus (Carroll & Gaskill 1985, p. 371) the interclavicle lies entirely posteroventral, i.e. superficial to the clavicular blades in *Serpianosaurus*.

The shape of the interclavicle of *Serpianosaurus* differs from the more plate-like appearance of the bone in the adult *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 16*a*), but resembles more closely the shape observed in *Neusticosaurus* or immature *Pachypleurosaurus* (Carroll & Gaskill 1985, fig. 16*b*). However, the shape of the interclavicle of *Serpianosaurus* shows some variability, as is also observed in *Neusticosaurus*, which might explain the controversy surrounding that bone (Peyer 1934). The interclavicle of *Serpianosaurus* typically forms a transverse and flattened bar of bone that is received in well-developed grooves or facets on the posteroventral aspect of the anteriomedial shanks of the clavicles (figure 8*e–h*). The latter bones meet in front of the interclavicle in a narrow and irregular suture: specimen T 96 shows quite distinctly a notched relation between the medioventral extremities of the clavicles. The interclavicle may vary somewhat in anteroposterior depth, and in particular it may develop a posteromedial extension (specimen T 3402).

The disarticulated clavicles of specimen T 1045 quite clearly document the general structure of these bones (figure 8*a*). The clavicle can be described as an angulated bone, consisting of an anteromedial and a posterolateral shank, connected by a broadened middle portion. The isolated left clavicle of specimen T 1045, measuring 40 mm in length, encloses with its two shanks an angle of about 120°. The anteromedial shank is somewhat curved and, in contrast to that of *Pachypleurosaurus*, it is relatively narrow in cross-sectional diameter as well as only slightly flattened. It meets its counterpart in an irregular medial suture, and receives the interclavicle on its posteroventral aspect.

The anteromedial shank of the clavicle turns into the posterolateral shank in the flattened and expanded middle portion of the bone. From this expanded middle portion the posterolateral shank emerges as a tapering projection that overlaps the dorsal (medial) surface of the broad ventral portion of the scapula (figure 8*d*). The extent of the overlap appears to be variable. In the large specimen T 3931, the posterodorsal shank of the clavicle forms a distinct projection that extensively overlaps the scapular blade; the same may be expected from the clavicle of specimen T 1045 to judge from its shape. A contrast is provided by the smaller specimen T 3680 where the posterodorsal shank of the clavicle is shorter and the overlap with the scapula accordingly less extensive. The size of the posterolateral projection of the clavicle might thus be related to the overall size of the specimen, i.e. to the age of the individual. However, some individual variation seems also to be involved because the posterolateral process of the clavicle is well developed in other relatively small specimens such as T 1071 and T 3933. A posterior projection of the clavicle overlapping the scapula is also observed in *Pachypleurosaurus* (Carroll & Gaskill 1985).

The relations of the scapula to neighbouring bones is well documented by the specimens T 3406 and T 3681 (ventral view) as well as T 3680 (dorsal view, figure 8*d*). Anteromedially, the rounded ventral portion of the scapula joins up with the broad middle portion of the clavicle

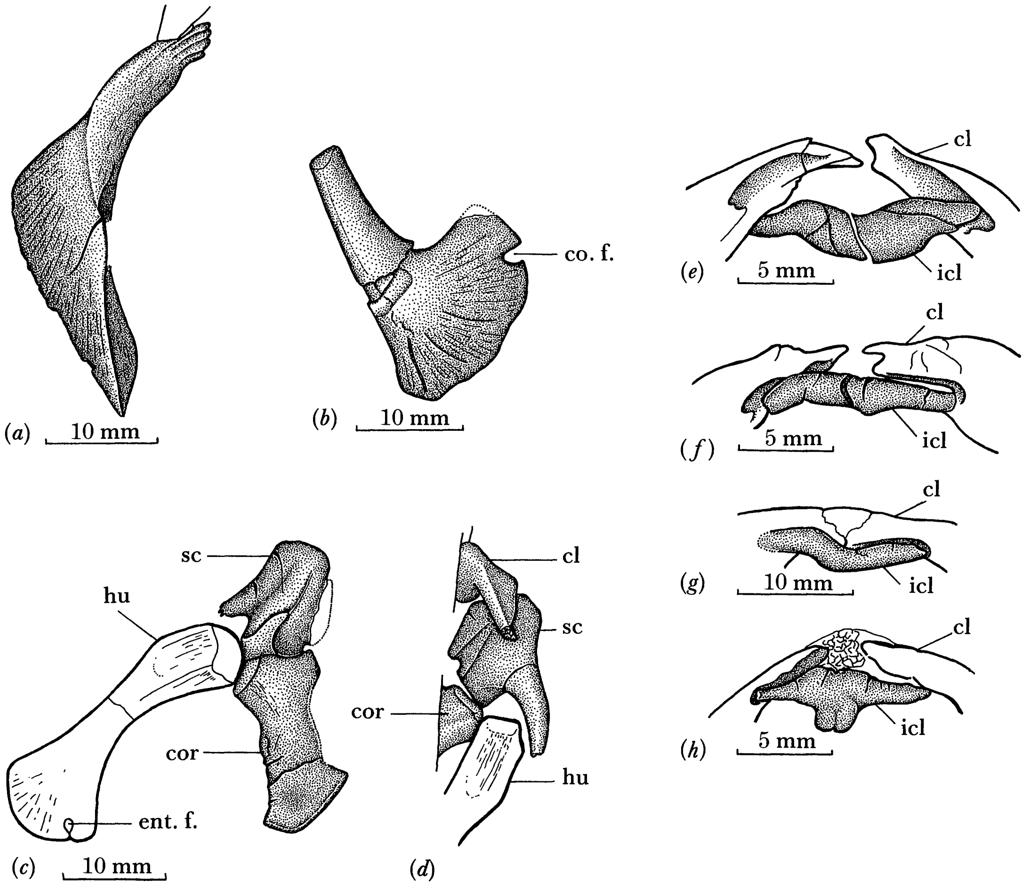

FIGURE 8. *Serpianosaurus mirigiolensis*, pectoral girdle. (*a*) Specimen T 1045, left clavicle in dorsal view; (*b*) specimen T 1045, right scapula in dorsal view; (*c*) specimen T 3681, scapulocoracoid in ventral view; (*d*) specimen T 3680, pectoral girdle in dorsal view; (*e*) specimen T 3676, interclavicle in ventral view; (*f*) specimen T 96, interclavicle in ventral view; (*g*) specimen T 3406, interclavicle in ventral view; (*h*) specimen T 3402, interclavicle in ventral view.

in a horizontal plane below the posterolateral shank of the latter bone. From the lateral aspect of the ventral scapular portion emerges the narrow dorsal blade at a level in front of the glenoid fossa. It is somewhat dorsoventrally compressed throughout its length. Specimen T 3406 shows that the dorsal scapular blade (or rather process) extended in a posterodorsal direction, but preservation precludes the determination of the exact angle. A distinct notch separates the dorsal blade from the scapular contribution to the glenoid fossa, which faces in a posterior and lateroventral direction. Because of its posterodorsal orientation, the scapular blade caused a rotation of the scapula following the compression of the fossils, and a consequent dislocation of the scapula relative to the coracoid.

A reconstruction of the relations between these two bones is nevertheless possible. The scapula meets the coracoid in a posterior suture of roughly transverse orientation. The ventrolaterally facing glenoid fossa is well exposed in specimen T 3681 (figure 8*c*). It demonstrates that the scapular contribution is more extensive and thus gives rise to a distinct ridge on the ventral surface of the scapula (also shown by specimen T 4406). The ridge on the ventral surface of the scapula, which forms the ventrolateral edge of the pectoral girdle, is less pronounced in *Pachypleurosaurus* and in *Neusticosaurus*. The ridge on the ventral surface of the scapula separates the insertional areas for dorsal and ventral pectoral muscles (Carroll & Gaskill 1985, p. 374).

Medial to the glenoid fossa, the smooth suture between scapula and coracoid extends in a transverse direction up to the posteromedial angulation of the ventral portion of the scapula. This posteromedial angulation is marked by a rounded notch that is much more distinct in *Serpianosaurus* than in either *Neusticosaurus* or *Pachypleurosaurus*. The scapular notch forms the anterolateral, anterior and medial margin of the coracoid foramen (figure 8*b*), which is completed posteriorly by the coracoid. In contrast to *Serpianosaurus*, the medial margin of the coracoid foramen remains unossified in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 374) and *Neusticosaurus*. Because of the dislocation of the scapula relative to the coracoid, it cannot be determined, however, whether the scapula did in fact meet the coracoid medial to the coracoid foramen, or whether a narrow gap still persisted.

The coracoid is of typical pachypleurosaurid shape. Its anterolateral corner contributes to the glenoid fossa; the articular surface faces in an anterior and lateroventral direction. Medial to the glenoid, the coracoid meets the ventral part of the scapula in a straight transverse suture. The anteromedial angulation forms the posterior and posterolateral margin of the coracoid foramen. The middle portion of the coracoid is typically constricted, with the concavity of the medial margin being more strongly expressed than that of the lateral margin. The posterior expansion of the coracoid is angulated: the posteromedial edge participates in the formation of the medioventral symphysis between the two coracoids. The posterior edge forms the straight and transversely orientated posterior margin of the pectoral girdle.

Peyer (1934) emphasized that *Phygosaurus* differs from other pachypleurosaurids in having a relatively longer medioventral symphysis between the two coracoid plates. Zangerl (1935) noted, however, that a similar extension of the coracoid symphysis is observed in the geologically youngest pachypleurosaurids from Monte San Giorgio, now recognized as *Pachypleurosaurus edwardsii* (Carroll & Gaskill 1985). *Serpianosaurus* falls into the same range of variability. This is corroborated by a comparison of specimen T 3460 of *Pachypleurosaurus*, showing a well-preserved pectoral girdle in ventral view, with *Serpianosaurus*. Although it is difficult to take precise measurements of the total length of the coracoid and of symphyseal length because of the rounded edges of the bones, the total length : symphyseal length ratio obtained for *Pachypleurosaurus edwardsii* falls into the range of variability observed in *Serpianosaurus*.

Humerus

The shape of the humerus of *Serpianosaurus* corresponds to the general pachypleurosaurid pattern. It is the strongest bone in the limb skeleton (Deecke 1886, p. 183), constricted medially but expanded at the proximal and distal ends, and only weakly curved if at all (figure 9). Carroll & Gaskill (1985, p. 375) have given a description of a three-dimensionally preserved humerus of *Pachypleurosaurus edwardsii*, which also applies in general terms to the humerus of *Serpianosaurus*. The proximal head is not dorsoventrally flattened as is the distal head; the proximal articular surface is broadly oval in outline. The expanded distal head is dorsoventrally flattened, and its articular surface is smoothly convex or even slightly angulated to separate the areas of contact with the radius and ulna. There is no indication of an expansion of the radius and ulnar articulation on to the ventral surface of the humerus, as is indeed to be expected in an aquatic reptile. The ability to flex the lower limbs was not strongly developed.

As in *Pachypleurosaurus*, there is no ectepicondylar foramen but only a shallow groove lateral to the ectepicondylar ridge (specimens T 3685 and T3931) whereas the entepicondylar foramen, lying well proximal to the distal articular surface, is fully surrounded by bone in all specimens. It must be noted, however, that the distance of the entepicondylar foramen from the distal articular surface tends to increase with increasing size of the specimen, although some individual variation has also to be taken into account. Specimen T 1071 (figure 9*b*) with a glenoid–acetabulum length of approximately 77 mm shows the entepicondylar foramen to lie right on the margin of the distal articular surface of the humerus (sex *x*, humerus length 18.2 mm), whereas in specimen T 3685 (figure 9*d*, *e*) with a glenoid–acetabulum length of approximately 82 mm, the entepicondylar foramen lies well proximal to the distal articular surface of the humerus (sex *y*, humerus length 22.4 mm). In specimen T 3931, with a glenoid–acetabulum length of approximately 148 mm and a humerus length of 35.7 mm, the entepicondylar foramen lies closer to the distal articular surface than in specimen T 1045 with a glenoid–acetabulum length of approximately 187 mm and a humerus length of 45 mm.

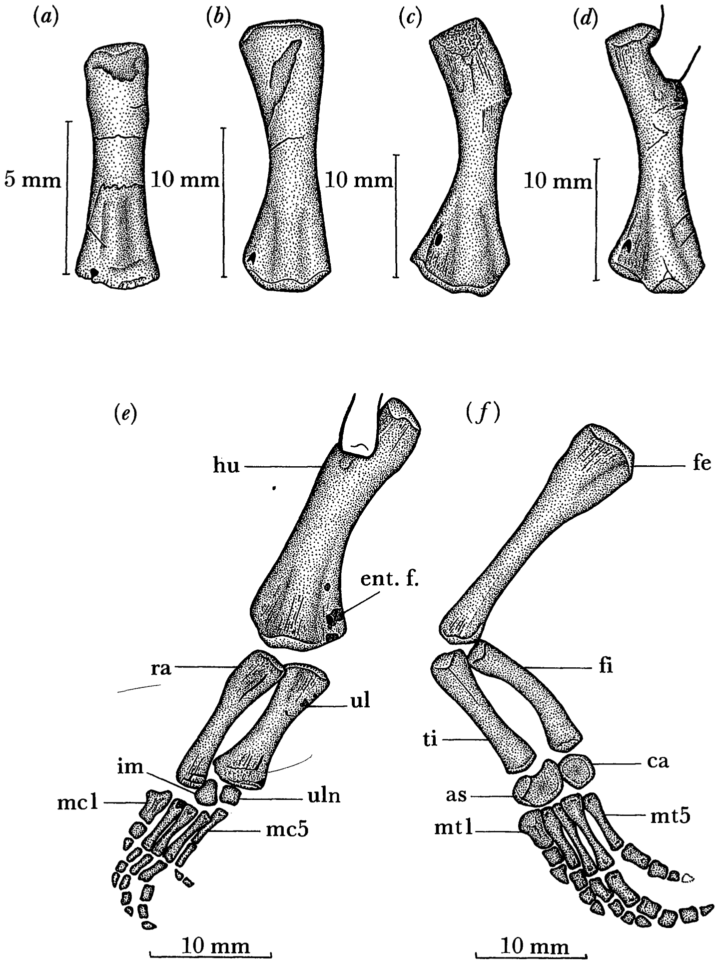

FIGURE 9. *Serpianosaurus mirigiolensis*, the appendicular skeleton. (*a*–*d*): Growth and sexual dimorphism in the differentiation of the right humerus, dorsal view (*a*, specimen T 132, juvenile; *b*, specimen T 1071, sex *x*; *c*, specimen T 3042, sex *y*; *d*, specimen T 3685, sex *y*); (*e*) specimen T 3685, left forelimb in dorsal view; (*f*) specimen T 3933, left hindlimb in dorsal view.

As in *Neusticosaurus*, and probably also in *Pachypleurosaurus*, the shape and relative length of the humerus indicates a sexual dimorphism in *Serpianosaurus* (figure 9*a–d*). Sex *x* is characterized by a relatively shorter humerus, with a hardly visible deltoid crest, no posterior angulation of the humeral shaft, and a less extensive distal expansion due to a lesser development of the entepicondyle. Sex *y* is characterized by a relatively longer humerus. The deltoid crest is well developed on the posterodorsal aspect of the shaft, where it may even produce a conspicuous tubercle for muscle attachment, giving the posterior margin of the humeral shaft an angulated appearance. The humerus is distally more conspicuously expanded, this being mainly due to an extended development of the entepicondyle.

One problem of the identification of sexual dimorphism is that it is overlapped by a positive allometric growth of the humerus. Sex *x* might represent nothing but juvenile individuals, and indeed the specimens representing sex *x* in the sample studied are few and all of relatively small size: the largest unequivocal representative of sex *x* shows a glenoid–acetabulum length of 103 mm (specimen T 97; humerus length 25 mm) compared with the largest specimen (T 1045) representing sex *y* with a glenoid–acetabulum length of 187 mm (humerus length 45 mm). However, the postulated sexual dimorphism is not just a misinterpretation of allometric growth: specimen 3402 with a glenoid–acetabulum length of 75 mm is slightly smaller than specimen 1071 with a glenoid–acetabulum length of 77 mm, and yet the humerus of T 3402 (length 23.7 mm) clearly indicates sex *y*, whereas T 1071 represents sex *x* (humerus length 18.2 mm). It thus appears that the sexual dimorphism is not only expressed by the relative size and shape of the humerus, but also the overall body size, sex *x* remaining generally smaller than sex *y*.

Radius and ulna

The radius is typically preserved in a position lateral to the ulna as in *Pachypleurosaurus*, so that the extensor surface of the lower limb is exposed dorsally. The radius differs from the ulna both by its shape and its greater length (figure 9*e*). The proximal third of the radius is broad relative to the middle and distal portions; the expansion of the proximal third produces an angulation on the lateral (outer) margin. The medial (inner) margin of the radius is straight or weakly concave. Distally, the radius projects beyond the ulna.

The ulna is generally thicker than the radius except for the latter's expanded proximal portion. Both the lateral and medial margins of the ulnar shaft are concave, whereas the proximal and distal articular surfaces are convex. The proximal head is slightly broader than the distal head. As in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 375), an ossified olecranon is lacking, what permitted a straight lateral position of the ulna relative to the humerus. The humerus:radius ratio varies from 1.53 (specimen T 132, juvenile) to 2.12 (specimen T 3402, sex *y*).

Manus

Serpianosaurus consistently shows two ossified elements in the carpus. These are of equal size, flat and of rounded contours. Their usual position as preserved is distal to the ulna and medial to the distal head of the radius which projects beyond the ulna (figure 9*e*). They are correspondingly identified as ulnare and intermedium. Carroll & Gaskill (1985, p. 375) were able to identify a third tiny bone of uncertain homology in the carpus of *Pachypleurosaurus*, which apparently failed to ossify in *Serpianosaurus*. The somewhat greater degree of ossification in the carpus of *Pachypleurosaurus* might be related to its greater overall size.

The metacarpals are particularly well exposed in the specimens T 96, T 1071, T 3676, T 3685 and T 3931. As in *Pachypleurosaurus*, the 1st metacarpal is much shorter and broader than the others; its length is just about half that of the second metacarpal, and its proximal head is distinctly expanded. In *Pachypleurosaurus*, it is the 3rd metacarpal that is the longest (Carroll & Gaskill 1985, p. 377). This is also the case in *Serpianosaurus* (particularly specimen T 96), but the difference is sometimes very small (specimens T 3931, T 3676), and the 3rd and 4th metacarpal may indeed be of equal length (specimen T 3685). The proximal heads of the metacarpals are slightly overlapping.

The phalangeal count in the manus is 2 - 3 - 4 - 4 - 3 (specimens T 1071, left manus; T 3685, left manus (figure 9*e*)). The presence of a 5th phalanx in the 4th digit, as it is exceptionally recorded in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 377), has to be inferred for the right manus of specimen T 3676 of *Serpianosaurus* (only four phalanges are counted in the 4th digit, but the shape of the 'terminal' phalanx suggests that the ungual phalanx is missing). The phalangeal count in the manus of *Serpianosaurus* is similar to that of *Neusticosaurus*, where some further reductions may occur, however (Sander 1989). The autopodium of *Pachypleurosaurus* again shows further reductions, the phalangeal count being 1 - 2 - 3 - 4(5) - 2(3) (Carroll & Gaskill 1985, p. 348, 377).

Pelvic girdle

The pelvic girdle of *Serpianosaurus* includes a relatively small ilium, which is constricted dorsally as is typical for nothosaurs in general. The ilium is well preserved in dorsal view in the specimens T 1045 (figure 10*d*) and T 3931. The broadened ventral portion of the bone contributes to the acetabulum; dorsally, the ilium is reduced to a short and tapering posterior process. Typically, three sacral ribs converge on the medial side of the dorsal portion of the ilium (figure 10*a*), but in some specimens a fourth rib (last sacral or first caudal) may be applied to the posterior tip of the bone (specimens T 951 (figure 10*b*), T 3675, T 3676, T 3677, T 3680, T 3931). The participation of the ilium in the formation of the acetabulum cannot be studied in detail in any of the specimens. The ventral exposure of the ilium, as seen in specimen T 3402, shows the bone to be moderately widened in its ventral part: its width only slightly surpasses that of the proximal head of the femur.

The pubis is an essentially flat bone, constricted in its middle portion, expanded towards its extremities. It is well exposed in dorsal view in specimen T 1045 (figure 10*d*), and in ventral view in specimen T 3402 (figure 10*c*). The dorsal margin of the pubis is weakly angulated. The longer shank of the angle established contact with the anterior part of the ilium; the shorter shank slants ventrally, and formed the suture with the ilium below the acetabular facet. Ventrally, the pubis is again weakly angulated, with the longer (posterior) shank meeting its counterpart in a medioventral symphysis that closed the large thyroid foramen anteriorly. The anteroventral edge of the pubis may be set off as a broad projection, especially in smaller specimens (T 3402, T 3406, T 3679, T 3680); in the larger specimens (T 1045, T 3931), the anteroventral edge of the pubis is no longer set off as a more or less distinct projection.

The ischium is of a similar general shape as the pubis, although somewhat more slender. In particular, the proximal (dorsal) part, meeting the posteroventral part of the ilium as well as the pubis, is narrower, and the middle portion is more conspicuously constricted. The broad distal expansion of the ischium is again weakly angulated, with the longer anterior shaft forming the medioventral symphysis with its counterpart which closes the thyroid foramen posteriorly.

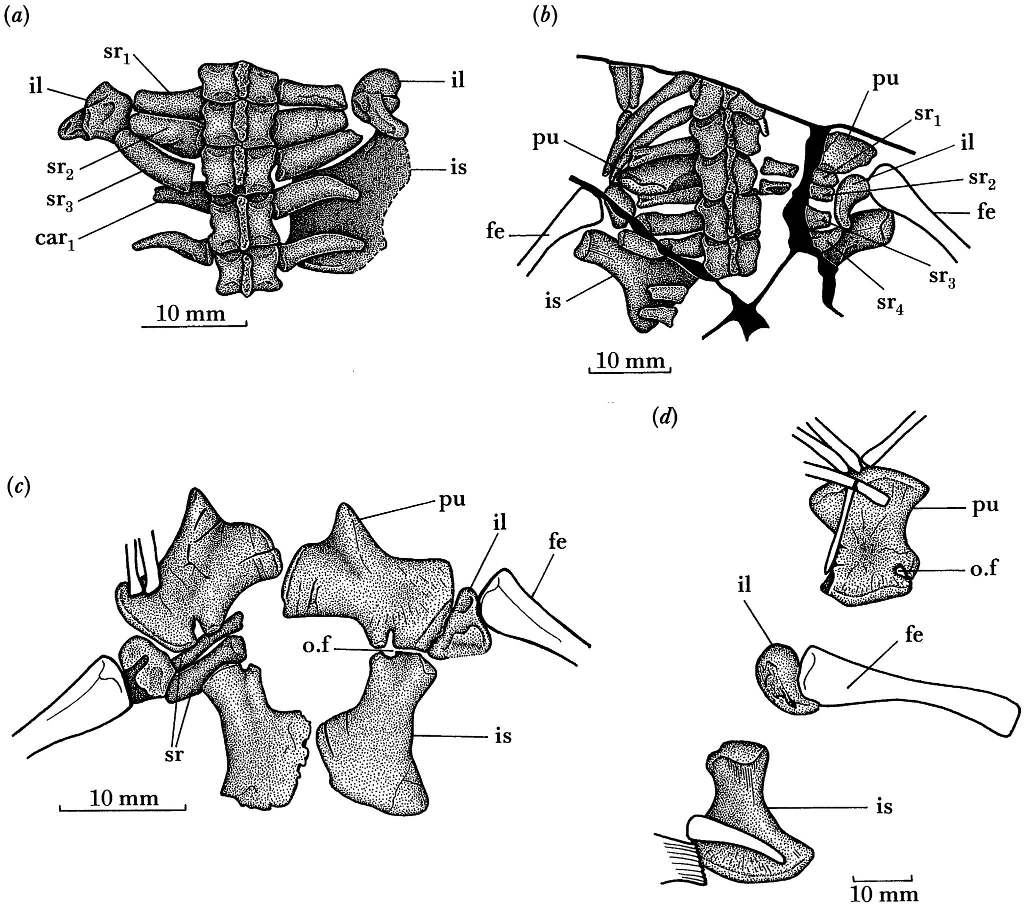

FIGURE 10. *Serpianosaurus mirigiolensis*, sacrum and pelvic girdle. (*a*) Specimen T **1071**, sacral region in dorsal view; (*b*) specimen T **951**, sacral region in dorsal view; (*c*) specimen T **3402**, pelvic girdle, ventral view; (*d*) specimen T **1045**, pelvic elements, dorsal view.

Pubis and ischium are separated by a large thyroid foramen except for the relatively narrow bridge formed by the two bones below the ilium, forming the ventral margin of the acetabular facet. The obturator foramen lies in the posterior margin of the pubis close to the suture with the ischium, just distal to the acetabulum. Its position in *Serpianosaurus* is variable, and apparently age related. In *Pachypleurosaurus*, the obturator foramen appears as a narrow slit in the posterior margin of the pubis (Carroll & Gaskill 1985, p. 379). In *Neusticosaurus*, the obturator foramen is either open, or it is closed narrowly. In small specimens of *Serpianosaurus* (T 3402 (figure 10*c*), T 3679), the obturator foramen forms a slit in the posterior margin of the pubis, closed posteriorly by the ischium, which may itself be weakly notched (specimen T 3402 (figure 10*c*)). In large individuals (specimen T 3931) of *Serpianosaurus*, however, the obturator foramen tends to be fully enclosed by the pubis, well set off from the posterior margin of the bone and hence from a contact with the ischium. The pubis fails to co-ossify fully behind the obturator foramen. Individual variation must also be taken into account, however. Specimen T 3678 (the glenoid–acetabulum length cannot be determined) is relatively small, but it shows an obturator foramen that is fully enclosed by the pubis and well set off from the posterior margin of the bone. The relatively small specimen T 3681 (glenoid–acetabulum length 88 mm) shows a narrowly closed obturator foramen in the left pubis, whereas that in the right pubis appears to stay open. A similar variation is observed in the relatively large specimen T 1045 (glenoid–acetabulum length of approximately 187 mm) with a narrowly closed obturator foramen in the right pubis, whereas that of the left pubis is open and slit-like.

Femur

The femur is typically less well developed than the humerus; it is usually somewhat shorter (in larger specimens), and the areas of muscle attachment are less conspicuous than on the humerus (in sex *y*). The shaft of the femur is biconcave, the proximal head is expanded to a greater degree than the distal head (figure 9*f*). The femur appears dorsoventrally flattened, particularly towards the proximal and distal extremities. A very shallow intertrochanteric fossa may be present. Carroll & Gaskill (1985, p. 379) described a horizontal posterior extension of the femur head in *Pachypleurosaurus*, which may have served the insertion of the iliofemoralis muscle. The same flat and posterior extension of the proximal femur head can be observed in both large (T 1045, right femur) and smaller (T 3933, left femur) specimens of *Serpianosaurus*; it is this expansion that causes the greater width of the proximal femur head compared with the distal one.

The ratio of humerus to femur varies in *Serpianosaurus* from 0.75 (specimen T 3810, sex *x*) to 1.24 (specimen T 3679, sex *y*; these ratios are size- and sex dependent: see below). The values fall into the range of variability observed in *Neusticosaurus* but they lie below the values obtained in *Pachypleurosaurus*, which range from 1.13 to 1.85 (Carroll & Gaskill 1985).

Tibia and fibula

Of the two lower limb elements, the fibula is usually the longer and slightly more massive bone (although the difference is minimal in specimen T 3933 (figure 9*f*)). The fibula is also easily distinguished from the tibia by its pronounced curvature, which contrasts with the rather straight tibia. The interosseal space is defined by the weakly concave lateral edge of the tibia and the strongly concave medial edge of the fibula. The proximal and distal expansions of the tibia are of about equal width, whereas the distal expansion of the fibula tends to be a little wider than the proximal expansion in most specimens. The difference is not as marked, however, as it is in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 381 and fig. 20).

Pes

As in *Pachypleurosaurus* (Carroll & Gaskill 1985, p. 381), two elements consistently ossify in the tarsus of *Serpianosaurus* (figure 9*f*). Of these, the astragalus is consistently larger than the calcaneum. The astragalus lies distal to the tibia, the distal head of which is received in a distinct facet on the astragalus. Laterally, distally and medially, the astragalus is of circular outline. The calcaneum is of an essentially circular outline, it lies distal to the fibula. Only the area of contact between astragalus and calcaneum may be flattened on both bones. In the left pes of specimen T 3931, the two elements are in articulation: no trace of a perforating foramen is observed.

In the metatarsal series it is again the 1st element that is distinctly shorter and broader than all the others (figure 9*f*): as in the case of the metacarpals, the 1st metatarsal is just about half the length of the 2nd, or even less, and the proximal head is markedly expanded. Unlike the condition observed in the manus, it is the 4th metatarsal that is consistently the longest element in the metatarsal series. The proximal heads of the metatarsals are slightly overlapping.

The phalangeal count is difficult to establish because few specimens show complete feet. Specimen T 1071 shows a superbly preserved right pes that documents the primitive phalangeal count 2 - 3 - 4 - 5 - 4; the same count is obtained in specimen T 3676 (right foot, with one terminal phalanx missing on the 4th toe) and in specimen 3933 (left foot with one terminal phalanx missing on the 5th toe (figure 9*f*)). Again, *Serpianosaurus* shows the most complete phalangeal count in the pachypleurosaurid genera from Monte San Giorgio. In *Neusticosaurus*, the primitive phalangeal count may also be preserved. In *Pachypleurosaurus*, the phalangeal count is 1 - 2 - 3(4) - 4(5) - 3 (Carroll & Gaskill 1985, p. 381).

Pachypleurosaurus differs from both *Serpianosaurus* and *Neusticosaurus* not only by the reduced number of phalanges in the 1st and 2nd digit of both manus and pes, but also by the length of the 1st phalanges in the digits 2, 3 and 4 relative to the corresponding metacarpals and metatarsals both in manus and pes. In *Pachypleurosaurus*, these phalanges are almost as long as the corresponding metacarpals or metatarsals, whereas both in *Serpianosaurus* and in *Neusticosaurus* the 1st phalanges of digits 2, 3 and 4 are distinctly shorter than the corresponding metacarpals or metatarsals respectively.

In *Serpianosaurus* the ratio of the 2nd metacarpal to the 1st phalanx in digit 2 varies from 2.44 to 3.62; the ratio of the second metatarsal to the 1st phalanx in the 2nd toe varies from 2.59 to 4.3. The 2nd metatarsal thus tends to be somewhat longer relative to the corresponding 1st phalanx than the 2nd metacarpal.

Size and proportions

The quantitative analysis presented in the following paragraph is based on measurements defined and tabulated in Appendix 1.

Size

The smallest individual of *Serpianosaurus* is the juvenile specimen T 132, with a glenoid–acetabulum length of approximately 41 mm; the largest specimen is T 1045 with a glenoid–acetabulum length of approximately 187 mm. The sample thus covers a wide size range and consequently permits the investigation of growth phenomena.

The size range does not extend evenly over the two sexes: sexual dimorphism is expressed not only in the differentiation of the humerus, but also in overall size. For those specimens that can be sexed by the relation of minimal width to distal width of the humerus (see below) the size for the sex *x* ranges from 77 mm to 103 mm glenoid–acetabulum length; sex *y* extends over a glenoid–acetabulum length of 60 mm to 187 mm.

Serpianosaurus, and in particular sex *y*, thus attains a larger overall size than *Neusticosaursus*. *Pachypleurosaurus*, however, is recorded to grow to a glenoid–acetabulum length of up to 295 mm (Carroll & Gaskill 1985, table 2), and thus attains even larger overall size.

Relative head length

Head length : glenoid–acetabulum length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.43 (specimen T 1045, sex *y*) to 0.57 (specimen T 3677, sex *y*) or 0.65 respectively (specimen T 132, juvenile); no sexual dimorphism is expressed by this ratio.

An interesting point to note is the ratio of the juvenile specimen T 132, which is distinctly higher. This indicates a negative allometric growth of the head compared with the trunk.

In *Pachypleurosaurus*, the same ratio varies from 0.20 to 0.45 (Carroll & Gaskill 1985, table 3); this shows that *Serpianosaurus* differs from *Pachypleurosaurus* by a relatively longer head (lower jaw).

The ratio values tabulated by Carroll & Gaskill (1985, table 3) for *Neusticosaurus* indicate the same fact: the values are generally lower, showing that adult to subadult *Neusticosaurus* are again characterized by a relatively shorter head as opposed to *Serpianosaurus*. Only the values obtained for juvenile specimens extend up into the range of ratios of *Serpianosaurus*, expressing nothing but the positive allometric growth in the first genus, too.

The relatively long head (lower jaw) is indeed a diagnostic feature of the genus *Serpianosaurus*, readily visible upon superficial inspection of the fossils.

Head length: standard length ratio

The range of variability recorded for *Serpianosaurus* extends from 1.94 (specimen T 3406, sex *y*) to 2.77 (specimen T 132, juvenile); the high value obtained for the juvenile again testifies to the negative allometric growth of the head as opposed to standard length, assumed to grow isometrically (Tschanz 1986). No sexual dimorphism is expressed by this ratio.

The ratio of adult to subadult *Neusticosaurus* again extends to somewhat lower values than are recorded for *Serpianosaurus*, indicating a somewhat smaller head in the first genus.

The comparison with *Pachypleurosaurus* must be based on the standard length as defined by Carroll & Gaskill (1985): the skull length must be related to the length of the centrum of a posterior dorsal vertebra (p.t.c., posterior trunk vertebra). This is possible with some accuracy only in specimens preserving the posterior trunk vertebrae in lateral or ventral view, which are 10 out of the entire sample of *Serpianosaurus*. The skull length: p.t.c. ratio changes from 8.14 (specimen T 1045) to 10.02 (specimen T 3676) in *Serpianosaurus*; these values are distinctly higher than those recorded for *Pachypleurosaurus* (Carroll & Gaskill 1985, table 3), testifying to the fact that *Serpianosaurus* is characterized by a larger head than *Pachypleurosaurus*.

Head length: humerus length ratio

The ranges of ratios recorded for *Serpianosaurus* extends from 1.59 (specimen T 3677 sex *y*) to 2.40 (specimen T 3684, sex *x*) and 3.45 (specimen T 132, juvenile) respectively. No sexual dimorphism is expressed by this ratio.

The large ratio obtained for the juvenile specimen T 132 again demonstrates the negative allometric growth of the head, coupled with a positive allometric growth of the humerus (see below).

The values obtained for adult or subadult *Neusticosaurus* indicate a relatively shorter head in this genus.

The values for the corresponding ratio given for *Pachypleurosaurus* by Carroll & Gaskill (1985, table 3) are distinctly lower, ranging from 0.71 to 1.53. This indicates that the latter genus is characterized either by a smaller head, or by a longer humerus. The head length: glenoid–acetabulum length and head length: p.t.c. ratios have demonstrated that the head of *Pachypleurosaurus* is indeed relatively shorter, whereas the analysis of limb proportions below will show that the humerus of *Pachypleurosaurus* is not relatively longer compared with *Serpianosaurus*.

Forelimb proportions

Humerus length : glenoid–acetabulum length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.19 (specimen T 132, juvenile) to 0.36 (specimen T 3742, sex *y*). No sexual dimorphism is expressed by this ratio.

The low value recorded for the juvenile specimen T 132 demonstrates the positive allometric growth of the humerus during ontogeny.

The ratio obtained for adult to subadult *Neusticosaurus* (Sander 1989) and *Pachypleurosaurus* (Carroll & Gaskill 1985, table 3) overlap with the range of ratios obtained for *Phygosaurus*.

Humerus length : standard length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.80 (specimen T 132, juvenile) to 1.48 (specimen T 3742, sex *y*).

For those specimens sexed by the relation of minimum humerus width to distal width of the humerus (see below), the humerus length:standard length ratio in sex *x* extends from 0.99 (specimen T 1071) to 1.13 (specimen T 97); the values for sex *y* range from 1.13 (specimen T 3685) to 1.48 (specimen T 3742).

The low ratio obtained for the juvenile specimen T 132 again testifies to the positive allometric growth of the humerus.

The values of this ratio obtained for adult to subadult *Neusticosaurus* (Sander 1989) overlap with the range of ratios recorded for *Serpianosaurus*.

The comparison with *Pachypleurosaurus edwardsii* must again be based on the standard length as defined by Carroll & Gaskill (1985), which means that the humerus length is to be related to the length of the posterior trunk centrum. The values obtained for *Serpianosaurus* range from 4.54 (specimen T 1045; the ratio is 3.73 in the poorly preserved specimen T 3801, the measurement of which may be inaccurate) to 5.9 (specimen T 3677); the corresponding ratios for *Pachypleurosaurus* (Carroll & Gaskill 1985, table 3) fall into the range of variation recorded in *Serpianosaurus*.

Humerus length : femur length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.75 (specimen T 3810, sex *x*) to 1.24 (specimen T 3679, sex *y*). The juvenile specimen T 132 again shows a relatively short humerus, with a ratio of 0.83 (specimen T 3810, sex *x*, which has an even lower value than T 132, is a small and poorly preserved specimen from Point 902, yet larger than T 132).

For those specimens sexed by the relation of minimum humerus width to distal width of the humerus, the humerus length:femur length ratio in sex *x* ranges from 0.75 (specimen T 3810) to 1.05 (specimen T 96); for sex *y*, the values range from 0.98 (specimen T 3685) to 1.24 (specimen T 3679). The values for sexes *x* and *y* are overlapping.

The genus *Neusticosaurus* yielded similar values for that ratio in subadult or adult specimens, again segregated into sexes (Sander 1989).

In contrast, the values recorded for *Pachypleurosaurus* by Carroll & Gaskill (1985, table 3) are distinctly higher than the values obtained for *Serpianosaurus*. This must mean that *Pachypleurosaurus* either has a longer humerus, or a shorter femur. The humerus of the latter genus was shown above to be of similar length relative to the trunk as in *Serpianosaurus*; in contrast, the femur of *Pachypleurosaurus* is distinctly shorter relative to the trunk and relative to the length of the posterior trunk centrum than in *Serpianosaurus* (see below). *Pachypleurosaurus* therefore is characterized by a relatively shorter femur.

Humerus length : length of metacarpal 3 *ratio*

The range of ratios recorded for *Serpianosaurus* extends from 3.39 (specimen T 132) to 5.51 (specimen T 3676, sex *y*). The low value recorded for the juvenile specimen T 132 is correlated with the positive allometric growth of the humerus.

A weak sexual dimorphism is expressed in this ratio. Among the specimens sexed by the relation of minimal to distal width of the humerus, the above ratio varies from 3.94 (specimen T 951) to 4.37 (specimen T 96) in sex *x*; the values for sex *y* range from 3.78 (specimen T 3406) to 5.51 (specimen T 3676).

The ratios recorded for *Neusticosaurus* overlap with those of *Serpianosaurus* (Sander 1989).

The humerus length has been inversely related to the length of the 3rd metacarpal by Carroll & Gaskill (1985). The length of 3rd metacarpal : humerus length ratio ranges from 0.18 to 0.3 in *Serpianosaurus*, and thus encompasses the values obtained for *Pachypleurosaurus* by Carroll & Gaskill (1985, table 3). However, *Serpianosaurus* attains higher values than the latter genus, which indicates either a longer metacarpal 3, or a shorter humerus. This phenomenon is coupled with the inclusion of smaller specimens in the *Serpianosaurus* sample: the highest ratio value, viz. 0.295, is recorded for the juvenile specimen T 132 with a relatively short humerus, because of the latter's positive allometric growth.

Humerus length : radius length ratio

The range of ratios recorded for *Serpianosaurus* extends from 1.53 (specimen T 132, juvenile) to 2.12 (specimen T 3402, sex *y*); the low value recorded for the juvenile specimen T 132 is due to the positive allometric growth of the humerus.

A weak expression of sexual dimorphism may be expected in that ratio, too, as humerus length is involved. Indeed, among the specimens sexed by the relation of humerus minimal width to humerus distal width, the values for sex *x* range from 1.56 (specimen T 951) to 1.80 (specimen T 96), whereas the values for sex *y* range from 1.59 (specimen T 1834) to 2.12 (specimen T 3402).

Again, the radius was inversely related to the humerus for *Pachypleurosaurus* by Carroll & Gaskill (1985). The radius length : humerus length ratio ranges from 0.47 and 0.66 in *Serpianosaurus*; the values obtained for *Pachypleurosaurus* fall into this range of ratios (Carroll & Gaskill 1985, table 3), although the first genus attains both lower and higher values. This is partly because of the inclusion of the small specimen T 132 in the sample of *Serpianosaurus*.

Humerus length : humerus distal width ratio

The range of ratios recorded for *Serpianosaurus* extends from 2.27 (specimen T 81, sex *y*) to 3.66 (specimen T 3675, sex *y*). No sexual dimorphism is apparent in this ratio.

The range of ratios obtained for *Neusticosaurus* (Sander 1989) overlaps with that of *Serpianosaurus*.

Radius length: standard length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.53 (specimen T 132, juvenile) to 0.78 (specimen T 3742); the low value obtained for the juvenile specimen T 132 indicates positive allometric growth of the radius.

The values obtained for *Neusticosaurus* (Sander 1989) overlap with those of *Serpianosaurus*.

Length of metacarpal 3: standard length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.23 (specimen T 1071, sex *x*) to 0.30 (specimens 3742, T 3406, sex *y*).

A weak sexual dimorphism is expressed in this ratio again. For specimens sexed by the relation of minimal humerus width to distal width, the above ratio varies from 0.23 (specimen T 1071) to 0.27 (specimen T 97) in sex *x*; for sex *y*, the values range from 0.25 (specimen T 3931) to 0.30 (specimens T 3742, T 3406).

Humerus minimal width: humerus distal width ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.36 (specimen T 3406, sex *y*) to 0.67 (specimen T 4076, sex *x*). It is this ratio that most clearly expresses the sexual dimorphism in *Serpianosaurus* (figure 11) which, as in other pachypleurosaurids, is ultimately correlated with the differentiation of the humerus (see morphological description above).

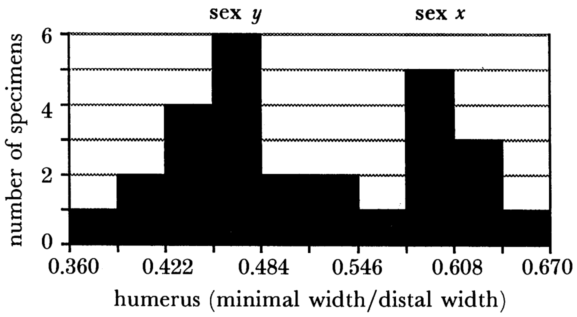

FIGURE 11. Sexual dimorphism in *Serpianosaurus* as expressed by the ratio of minimal to distal width of the humerus.

Sex *x* is immediately identified by a lesser distal expansion of the humerus, i.e. the entepicondyle is less well differentiated. This results in higher ratio values. For sex *x*, the values range from 0.58 (specimens T 3684, T 4115) to 0.67 (specimen T 4076). For sex *y*, the values range from 0.36 (specimen T 3406) to 0.54 (specimen T 3676). As a consequence of the positive allometric growth of the humerus, the juvenile specimen T 132 falls between the two sexes with a ratio of 0.57.

The ratio permits the sexing of the specimens. Nine specimens can be assigned to sex *x* (T 96, T 97, T 951, T 1071, T 3684, T 3807, T 3810, T 4076, T 4115) and 17 specimens represent sex *y* (T 81, T 1045, T 1834, T 3402, T 3406, T 3674, T 3675, T3676, T 3677, T 3678, T 3679, T 3681, T 3682, T 3685, T 3709, T 3742, T 3931). As mentioned in the morphological description, differences in humerus differentiation, if interpreted as an expression of sexual dimorphism, indicate a very uneven sex ratio for the Grenzbitumen population of *Serpianosaurus*, all other factors being equal.

Hindlimb proportions

Femur length : glenoid–acetabulum length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.21 (specimen T 1834, sex *y*) to 0.32 (specimen T 3742, sex *y*). No sexual dimorphism is expressed in hindlimb proportions.

The values recorded for *Neusticosaurus* (Sander 1989) fall into the range of ratios of *Serpianosaurus*, with some tendency to be concentrated at the lower end.

The values recorded for *Pachypleurosaurus* (Carroll & Gaskill 1985, table 3) are distinctly lower than those of *Serpianosaurus*, ranging from 0.16 to 0.25. This observation confirms the conclusion reached above that *Pachypleurosaurus* is characterized by a relatively shorter femur compared with *Serpianosaurus*.

Femur length : standard length ratio

The range of ratios recorded for *Serpianosaurus* extends from 0.97 (specimen T 132, juvenile) to 1.32 (specimen T 3742, sex *y*). No sexual dimorphism can be recognized in this ratio. As testified by the small value obtained for the juvenile specimen T 132, the femur might show slight positive allometric growth. However, the next largest value recorded is 0.98 (specimen T 3406; glenoid–acetabulum length 101 mm), showing that the juvenile specimen is set off by only a minor difference from larger specimens. As no allometric growth is indicated by the above ratio (femur : glenoid–acetabulum), it might be nothing but a sampling bias that the juvenile specimen shows the lowest value for the ratio of femur length : standard length.

The values recorded for *Neusticosaurus* (Sander 1989) fall into the range of ratios of *Serpianosaurus*.

Comparison with *Pachypleurosaurus* must again be based on the standard length as defined by Carroll & Gaskill (1985); the ratio ‘femur length : posterior trunk centrum’ length yields values for *Serpianosaurus* ranging from 4.54 (specimen T 1045; 3.73 in the problematical and poorly preserved specimen T 3810) to 5.90 (specimen T 3677). The values recorded for *Pachypleurosaurus* by Carroll & Gaskill (1985, table 3) are all distinctly lower, indicating the relatively shorter femur.

Length of metatarsal 4 *: standard length ratio*

The range of ratios recorded for *Serpianosaurus* extends from 0.33 (specimen T 3685: the 4th metatarsal is difficult to measure, and the ratio may be too low; the next value is 0.37, obtained in specimen T 1045, sex *y*) to 0.46 (specimen T 3742, sex *y*).

Femur length : fibula length ratio

The range of ratios recorded for *Serpianosaurus* extends from 1.56 (specimen T 1071, sex *x*) to 1.89 (specimen T 3682, sex *y*). A weak sexual dimorphism may be expressed in this ratio, although the values for the two sexes overlap broadly. The ratio of sex *x* ranges from 1.56 (specimen T 1071) to 1.76 (specimen T 96), whereas the values for sex *y* range from 1.70 (specimen T 3406) to 1.89 (specimen T 3682).

Since the ‘fibula length : standard length’ ratio does not indicate any segregation of the sexes, one may conclude that sex *x* is characterized by a somewhat shorter femur. However, the femur length as opposed to the standard length or glenoid–acetabulum length does not disclose a clearcut sexual dimorphism either. The partial segregation of the sexes in the present ratio values may thus represent nothing but a sampling bias.

The values recorded for *Neusticosaurus* (Sander 1989) overlap with the range of ratios of *Serpianosaurus*.

The comparison with *Pachypleurosaurus* must be based on the reversed relation of fibula to femur as calculated by Carroll & Gaskill (1985, table 3). The 'fibula:femur length' ratio ranges from 0.52 to 0.65 in *Serpianosaurus*; the values obtained for *Pachypleurosaurus* tend to be somewhat higher.

Femur length: length of metatarsal 4 ratio

The range of ratios recorded for *Serpianosaurus* extends from 2.54 (specimen T 132, juvenile) to 3.46 (specimen T 3685, sex *y*). The low value recorded for T 132 correlates with the relatively short femur in juvenile specimens. No sexual dimorphism is expressed by this ratio as judged over the entire range of variation.

The values recorded for *Neusticosaurus* (Sander 1989) overlap with the range of ratios of *Serpianosaurus*.

The ratio was calculated in an inverse sense for *Pachypleurosaurs* by Carroll & Gaskill (1985, table 3). The length of 'metatarsal 4:femur length' ratio varies from 0.28 to 0.39 in *Serpianosaurus*; values for *Pachypleurosaurs* are distinctly higher.

General conclusions

The quantitative analysis of the *Serpianosaurus* material included in the present study indicates the negative allometric growth of the skull and the positive allometric growth of the humerus. These are in fact characteristics observed in all pachypleurosaur taxa from the Middle Triassic of Monte San Giorgio, where the abundance of the material permits the study of growth. A complete growth series is available for the genus *Neusticosaurus* and will be described in detail by P. M. Sander (1989). The corollary of these results is that age and growth factors play an important role in pachypleurosaurid taxonomy (see table 1). The identification of taxa on body proportions in particular must take growth phenomena into account.

TABLE 1. COMPARISON OF *SERPIANOSAURUS* WITH ADULT OR SUBADULT *NEUSTICOSAURUS* (SANDER 1989) AND WITH *PACHYPLEUROSAURUS*

(Values for *Pachypleurosaurus* are taken from Carroll & Gaskill 1985, table 3. For abbreviations used see p. 73.)

	Serpianosaurus	*Neusticosaurus*	*Pachypleurosaurus*
head/glenoid–acetabulum	0.43–0.65	0.32–0.56	0.20–0.44
head/standard	1.94–2.73	1.39–2.29	0.80–1.76
head/p.t.c.	8.14–10.02	5.56–9.16	3.60–6.10
head/humerus	1.59–3.45	0.95–2.29	0.71–1.53
humerus/femur	0.75–1.24	0.88–1.30	1.13–1.82
femur/glenoid–acetabulum	0.21–0.32	0.21–0.30	0.16–0.25
femur/p.t.c.	4.54–5.90	2.96–5.8	2.6–3.2
fibula/femur	0.52–0.65	0.48–0.66	0.59–0.72
metatarsal 4/femur	0.28–0.39	0.34–0.45	0.45–0.51

Another point to emphasize with respect to body proportions of *Serpianosaurus* is sexual dimorphism, best expressed in the minimal width: distal width ratio of the humerus. The sexual dimorphism is also expressed by other ratios involving humerus length as opposed to overall size (glenoid–acetabulum length), standard length, radius length, length of metacarpal 3 and femur length. Sex *x* remains generally smaller and shows a weaker and relatively shorter humerus, with a less-well-developed entepicondyle compared with sex *y*.

The body proportions of *Serpianosaurus* broadly overlap with those of *Neusticosaurus* (Sander 1989) with the exception of the relatively longer skull diagnostic for the first genus (see table 1), compared with subadult and adult *Neusticosaurus*. If juvenile specimens of the latter genus were included in the comparison, the ratios involving skull length would extend to the values obtained for *Serpianosaurus*. Differences obtain, however, with respect to *Pachypleurosaurus* (Carroll & Gaskill 1985): *Serpianosaurus* is characterized by a smaller humerus length:femur length ratio and by larger values in the relation of femur length to body size (glenoid–acetabulum length and standard length). This indicates a relatively longer femur resulting in different limb proportions which will be analysed in greater detail by Sander (1989).

SEXUAL DIMORPHISM IN *SERPIANOSAURUS*

Sexual dimorphism in *Serpianosaurus* affects overall size as well as the relative size of forelimb elements. It is most pronounced in the relation of minimal width to distal width of the humerus because of the different size of the entepicondyle (see also table 2).

One problematical aspect of sexual dimorphism as recorded in *Serpianosaurus* concerns the great size difference between the two sexes (sex *x* remaining much smaller), correlated with an uneven sex ratio (sex *x* being much rarer). This raises the question whether the two forms, here interpreted as two sexes, might not represent two different species instead.

In his study of sexual dimorphism in reptiles, Fitch (1981) devised the female:male ratio (FMR) as a measure for sexual size difference. The FMR is calculated from the snout–vent length (SV) of the female related to that of the male expressed as a percentage:

$$(\mathrm{SV}_{\mathrm{female}}/\mathrm{SV}_{\mathrm{male}}) \times 100.$$

As a general result, Fitch (1981, p. 3) concluded that 'Females of different reptile species investigated ranged from about $\frac{2}{3}$ to $2\frac{1}{2}$ times mean male length'; 'In turtles and snakes it is most common for females to exceed males in average size, whereas in lizards the opposite relationship is more common' (Fitch 1981, p. 32).

To compare the sexual size difference of *Serpianosaurus* with that recorded in extant reptiles, the SV was averaged over all those specimens of sex *x* and *y* respectively that permitted appropriate measurements. With sex *x* interpreted as female, the FMR is 82; considering sex *y* as female, the FMR is 122. Both values fall into the range of ratios recorded within extant reptiles. To test an extreme FMR for animals that have certainly reached sexual maturity, the largest specimen of sex *x* (T 97; glenoid–acetabulum length 103 mm; SV 257 mm) was compared with the largest representative of sex *y* (T 1045; glenoid–acetabulum length 187 mm; SV *ca.* 390 mm). Treating sex *x* as female, the FMR is 65.8; considering sex *y* as female, the FMR is 151.7. Both values lie at the opposite extremes of the range of ratios recorded in extant reptiles. An FMR of 150 or more is approached by some turtles only (*Trionyx*), whereas the FMR of 65 lies at the lower end of variation, matched only by fully grown alligators and approached by some few, isolated, insular West Indian iguanids (*Anolis*, *Leiocephalus*).

In crocodiles and lizards it is the male that usually grows to larger size, whereas the opposite is true for turtles and snakes. Because of the similarity of the general body plan, it seems likely that female *Serpianosaurus* are represented by the smaller sex *x*. Fitch (1981) discussed several

Table 2. Proportions and sexual dimorphism in *Serpianosaurus*

(For abbreviations used see p. 73.)

ratio	total variation	sex *x*	sex *y*
head/glenoid–acetabulum	0.43–0.65	—	—
head/standard	1.94–2.77	—	—
head/humerus	1.59–3.45	—	—
humerus/glenoid–acetabulum	0.19–0.36	—	—
humerus/standard	0.80–1.48	0.99–1.13	1.13–1.48
humerus/femur	0.75–1.24	0.75–1.05	0.98–1.24
humerus/metacarpal 3	3.39–5.51	3.94–4.37	3.78–5.51
humerus/radius	1.53–2.12	1.56–1.80	1.59–2.12
humerus length/distal width	2.27–3.66	—	—
radius/standard	0.53–0.78	—	—
radius/ulna	1.04–1.20	—	—
metacarpal 3/standard	0.23–0.30	0.23–0.27	0.25–0.30
humerus min./distal width	0.36–0.67	0.58–0.67	0.36–0.54
femur/glenoid–acetabulum	0.21–0.32	—	—
femur/standard	0.97–1.32	—	—
fibula/standard	0.57–0.73	—	—
metatarsal 4/standard	0.33–0.46	—	—
femur/fibula	1.56–1.89	—	—
femur/metatarsal 4	2.54–3.46	—	—

explanations to account for distinct sexual size differences. In isolated insular West Indian anole species, habitat partitioning was observed between the sexes, which increases the potential carrying capacity of the habitat. Lizards also show a mating behaviour based on a repertoire of aggressive behaviour patterns: mating comes close to or even corresponds to rape, with dominant males occasionally raping subordinated individuals of the same sex to assert their social status (Noble & Bradley 1933). Relative size increase of males may enhance mating success.

On the other hand, Fitch (1981) demonstrated relative size increase of females in viviparous species. If sex *x* does in fact represent females, the relative small size of that sex might indicate that *Serpianosaurus mirigiolensis* was an oviparous species.

Comparison with the genus *Phygosaurus*

The pachypleurosaur material here named *Serpianosaurus* was informally referred to the genus *Phygosaurus* before its present description. At present, it is impossible to establish the reasons for this identification. A thorough comparison of *Serpianosaurus* and *Phygosaurus* nevertheless appears to be in order. However, the type and only known specimen of *Phygosaurus* can no longer be located; it may have been lost in a fire at the Geological Institute of the Strasbourg University in 1967 (letter from M. Wolf, Institut de Géologie, Université Louis Pasteur de Strasbourg, dated 12 May 1987). All comparison must rest on Peyer's (1934) work on the Strasbourg specimen, first described by Deecke (1886) and later designated as *Phygosaurus perledicus* by Arthaber (1924). The specimen comes from Perledo (Upper Ladinian – Lower Carnian) and therefore is geologically younger than *Serpianosaurus* (Anis–Ladin boundary). The stratigraphical precursor of *Phygosaurus* is *Pachypleurosaurus edwardsii*, representing the second taxon to be incorporated in a detailed comparison. The type of *Phygosaurus* comprises the posterior part of the cervical vertebral column as well as the entire dorsal portion, the pectoral girdle, most of the pelvic girdle and proximal parts of the forelimbs. Peyer (1934, p. 120) provided a diagnosis for the genus, but Zangerl (1935, p. 68) doubted its generic distinctiveness from *Pachypleurosaurus edwardsii* because some of the allegedly diagnostic features such as the oblong cross-sectional area of the proximal part of dorsal ribs or the extended coracoid symphysis are also observed in the Monte San Giorgio material from Alla Cascina (see Carroll & Gaskill (1985) for a monographic description).

The glenoid–acetabulum length of the Perledo specimen as figured by Peyer (1934, pl. 38, fig. 2) approximates 210 mm; it thus is somewhat larger than the largest specimen included in the Grenzbitumen sample. The size difference may be even more pronounced because Carroll & Gaskill (1985, p. 349) note the incomplete ossification of the distal end of the humerus and proximal end of ulna and radius. Other proportional values cannot be used in the comparison of the Strasbourg specimen because of its incompleteness. The genera *Neusticosaurus* and *Serpianosaurus* are fairly close with respect to their body proportions, whereas *Pachypleurosaurus edwardsii* as described by Carroll & Gaskill (1985) differs mainly in the relative size of the head and of the femur. Both structures are lacking in the Strasbourg specimen.

A superficial comparison of *Serpianosaurus* with the Strasbourg specimen as described and figured by Peyer (1934, pl. 38, fig. 2 and pl. 39) reveals several similarities.

The ribs lack pachyostosis, and the cross-sectional area of their proximal part is dorsoventrally flattened. The latter feature might – in some measure at least – result from *post mortem* compression of the fossils. In specimen T 3931 the ribs are distinctly flattened in their proximal part whereas in specimen T 1071 with an almost three-dimensional preservation this feature is far less distinctive.

The gastral ribs of the Strasbourg specimen are made up of five elements each (Peyer 1934), a feature also recorded for *Serpianosaurus*, but not for the genera *Neusticosaurus* and *Pachypleurosaurus* (Carroll & Gaskill 1985). Gastral ribs composed of five elements have also been recorded for *Anarosaurus* (B. Peyer, personal communication, quoted by Zangerl (1935), p. 68), a genus characterized by elongated teeth in the anterior parts of the upper jaws (Dames 1890) and by a rather short humerus as compared with the femur (Kuhn-Schnyder 1959, p. 652; Carroll & Gaskill 1985, p. 349), as well as by relatively large upper temporal fossae with a broad participation of the postorbital in the anteromedial margin (Jaekel 1910; Nopcsa 1928; Carroll 1981, p. 379, fig. 32).

Another feature characteristic of the Strasbourg specimen is the anterior part of the dermal pectoral girdle. In the original description of the fossil, Deecke (1886) believed he could identify an interclavicle of unusual shape, forming a small triangular bone intercalated between the two medioventral tips of the clavicles. Döderlein recognized the erroneous identification of the interclavicle by Deecke (1886), and indicated its correct position and shape in the semi-diagrammatic reconstruction of the pectoral girdle of the Strasbourg specimen reproduced in Steinmann & Döderlein (1890, fig. 770). As in *Serpianosaurus*, the interclavicle forms a relatively narrow and elongated bone positioned along the caudoventral margin of the medioventral shanks of the clavicles. The transversely elongated and narrow shape of the interclavicle, with the narrowness of the medioventral shanks of the clavicles, distinguishes the Strasbourg specimen, as well as *Serpianosaurus*, from *Pachypleurosaurus edwardsii* (cf. Zangerl (1935, fig. 32B) and Carroll & Gaskill (1985)). The shape of the interclavicle of *Serpianosaurus* shows some degree of variation, however, and a similar shape and variation is observed in *Neusticosaurus* (Carroll & Gaskill 1985, p. 349). What distinguishes the Strasbourg specimen, as well as *Serpianosaurus*, from *Neusticosaurus* is the straight transverse orientation of the interclavicle and of the anteromedial shanks of the clavicles, with a sharp angulation between the narrow anteromedial and the expanded posterodorsal parts of the clavicle. This is particularly well appreciated in ventral view: specimen T 3406, for example, closely corresponds to the Strasbourg specimen with respect to this feature, whereas in *Neusticosaurus* the anteroventral part of the dermal pectoral girdle appears more gently and evenly curved.

Peyer (1934, p. 96) determined the last cervical vertebra in the Strasbourg specimen by its position anterior to the clavicles. On this basis he obtained a total of 24 dorsal vertebrae. By using the same criterion for the demarcation of the dorsal from the cervical region in the vertebral column of *Serpianosaurus*, 20–23 dorsal vertebrae can be counted. Because of the poor reliability of the criterion for a subdivision of the vertebral column, the vertebral counts appear to be closely comparable. *Pachypleurosaurus edwardsii* seems to be characterized by somewhat lower figures (19 or 20 dorsal vertebrae are indicated by Carroll & Gaskill (1985, p. 367)). Peyer (1934, p. 120) included the presence of two 'lumbar vertebrae' in his diagnosis of *Phygosaurus* as based on the Strasbourg specimen; according to Deecke (1886) a single lumbar vertebra is observed. The problem of determination of the number of 'lumbar vertebrae' results from the fact that the size decrease of the ribs is gradual. Hoffstetter & Gasc (1969, p. 203) rigorously defined 'true' lumbar vertebrae in reptiles by the absence of ribs; on this definition no lumbar ribs are present in *Phygosaurus*. However, the Strasbourg specimen shows the ribs in articulation with the last two dorsal vertebrae to be distinctly shorter; the posterior pair of these 'lumbar' ribs is no longer curved and is positioned at a right angle to the long axis of the vertebral column. A similar condition is observed in *Serpianosaurus*, with specimen T 3933 resembling the Strasbourg specimen particularly closely.

The shape of the coracoid was likewise considered to be diagnostic for the genus *Phygosaurus* by Peyer (1934, p. 120). The coracoid is described as being distinctly constricted in its medial portion, whereas the coracoid symphysis is said to be longer compared with other pachypleurosaurs. The ratio of the maximal length (height) of the coracoid to its minimum width ranges from 2.65 (specimen T 3676) to 3.8 (specimen T 3931) in *Serpianosaurus* (a total of seven specimens were measured; the average value obtained was 3.13). Taking measurements from Peyer's (1934, pl. 39) figure of the Strasbourg specimen, the ratio of maximal length (height) to minimal width of the coracoid is 3.6. The Strasbourg specimen lies at the upper end of the size range of *Serpianosaurus*, being even a little larger than specimen T 3931 with a comparable coracoid shape. Whether or not the degree of medial constriction of the coracoid is age related, the value obtained for the Strasbourg specimen falls into the range of ratios recorded for *Serpianosaurus*.

The extended coracoid symphysis has been rejected as a diagnostic feature of *Phygosaurus* by Zangerl (1935, p. 68), who recorded a similar coracoid shape in *Pachypleurosaurus* from Alla Cascina (see also Carroll & Gaskill 1985, fig. 16*f*). Although it is difficult to measure accurately the length of the symphyseal margin in disarticulated coracoids, this was attempted in four well-preserved specimens of *Serpianosaurus*, and the values obtained were related to coracoid length (height). The ratio of coracoid length (height) to symphyseal length was recorded to vary from 1.5 (specimen T 3676) to 1.9 (specimen T 3402). The values obtained from Peyer's (1934, pl. 39) illustration of the Strasbourg specimen indicate a ratio of approximately 1.65, which again falls into the range of ratios for *Serpianosaurus*.

The obturator foramen in the pubis is described and figured as slit-like for the Strasbourg specimen (Deecke 1886; Peyer 1934). The differentiation of the foramen is highly variable in *Serpianosaurus* (see the morphological description above), the character in question therefore cannot be used for diagnostic purposes.

The humerus of the Strasbourg specimen is typically pachypleurosauroid, only slightly curved and constricted in its middle portion but expanded distally. Measurements taken from Peyer's (1934, pl. 39) illustration indicate the ratio of the minimal width to the distal width of the humerus as being 0.35. The specimen thus falls into the lowermost end of the range of variation of the *Serpianosaurus*: maximal distal expansion of the humerus is observed in specimen T 3406 with a ratio of 0.36. It should be remembered that this character is sex related, and the Strasbourg specimen obviously is a representative of 'sex *y*'. The ratio of humerus length to distal width is 2.45 for the Strasbourg specimen as figured by Peyer (1934, pl. 39), a value that again falls into the range of ratios for the Grenzbitumen pachypleurosaurs.

The conclusion therefore must be that in all its observable characteristics, the Strasbourg specimen cannot be separated from *Serpianosaurus*. However, the type of *Phygosaurus perledicus* differs from *Pachypleurosaurus edwardsii* by having more dorsal vertebrae, and by the structure of the gastral ribs which are composed of five elements. The gastral ribs of *Pachypleurosaurus edwardsii* are composed of three elements only, a synapomorphy shared with the genus *Neusticosaurus* (Rieppel 1987*a*). The relatively large number of dorsal vertebrae in the Strasbourg specimen is of particular interest because, just like the structure of the gastral ribs, it sets *Phygosaurus* off from *Pachypleurosaurus edwardsii*, which is the stratigraphical precursor of the Perledo pachypleurosaurs. The Strasbourg specimen from Perledo resembles the geologically older *Serpianosaurus* more closely than the younger pachypleurosaurs from Monte San Giorgio with respect to vertebral numbers.

Whereas *Phygosaurus* cannot be separated from *Serpianosaurus*, all of the identifiable similarities are of plesiomorphic status. Gastral ribs composed of five elements are also observed in *Claudiosaurus* (Carroll 1981), *Lariosaurus* and other nothosaurs such as *Ceresiosaurus* (Peyer 1934), in *Anarosaurus* (Peyer, quoted in Zangerl (1935, p. 68)) and most probably in *Dactylosaurus* (Nopcsa 1928; Sues & Carroll 1985, fig. 1B). On the basis of outgroup comparison, the incorporation of five elements in a gastral rib must be judged to represent the plesiomorphous condition that cannot be diagnostic. The same is true for the absence of rib pachyostosis in *Serpianosaurus* and in the Strasbourg specimen; rib pachyostosis is also absent in *Claudiosaurus* (Carroll 1981) and *Anarosaurus*. *Lariosaurus* is polymorphous in this feature, as is *Dactylosaurus*. In fact, the type of *Phygosaurus perledicus* is not diagnostic at the generic level at all, as its quality of preservation does not permit the detection of apomorphic characteristics that would allow the dermarcation of the genus from other relatively plesiomorphous pachypleurosaur genera. On the present state of knowledge it must therefore be concluded that the name *Phygosaurus* (and therefore *Phygosaurus perledicus* Arthaber, 1924) represents a *nomen dubium* as the name 'is not certainly applicable to any known taxon' (Blackwelder 1967, pp. 398 and 425). The erection of a new genus to include the Monte San Giorgio material is thereby justified.

Diapsid relations

In 1860, Richard Owen recognized affinities between nothosaurs, plesiosaurs and placodonts, which is why he included these reptiles with some other enigmatic fossils such as *Tanystropheus* within his order Sauropterygia (Owen 1860, p. 209).

Cope considered the Sauropterygia to be closely related to chelonians and rhynchocephalians and formalized this opinion by the erection of a taxon, Synaptosauria (Cope 1885, p. 246), including these groups. Cope's classification was criticized by Baur (1887), who classified the Rhynchocephalia with lizards, mosasaurs and snakes. The Synaptosauria were retained, including the Testudinata and the Sauropterygia.

In 1914, a full account of the osteology of the genus *Araeoscelis* from the Lower Permian of Texas was published by Williston, who emphasized the presence of a single (upper) temporal fenestra in this lizard-like form. This prompted a comparison with all other fossil and extant reptiles characterized by a single temporal opening, namely the 'Ichthyosauria, Sauropterygia, 'Pelycosauria', Placodontia, Therapsida, Squamata and, if Huene is correct, the Proganosauria' (Williston 1914, p. 391). Of these, the pelycosaurs and therapsids (Synapsida of modern authors) were immediately dismissed as possible relatives of the newly discovered genus because of the different position of the fenestra relative to the temporal bones of the skull. In a similar vein, the Sauropterygia (including nothosaurs and plesiosaurs) were removed from consideration as they could only have a remote relationship with *Araeoscelis*. *Protorosaurus* on the other hand was judged to show 'some remarkable resemblances to *Araeoscelis*'. The Squamata were not considered by Williston to be related to diapsids, but to some reptile with a single (upper) temporal opening instead; the cheek of lizards (and snakes) would have become opened up through emargination from below. A similar interpretation was given for the lower cheek region of ichthyosaurs, whereas the position of the upper temporal fenestra was considered to be possibly different from that observed in *Araeoscelis*. Williston (1914, p. 400) concluded that *Araeoscelis* had to be included within the Squamata as the separate suborder Araeoscelidia, 'co-ordinate with the Lacertilia and Ophidia', whereas the Protorosauria would have to be placed 'immediately before the Squamata in any serial classification of reptiles'.

It was not until 1917, however, that Williston formalized his view of reptile phylogeny and classification. 'One thing is evident: even earlier than the origin of the lower vacuity in the Diapsida a simple upper vacuity, as in lizards, had developed, but with the temporal region imperforate below' (Williston 1917, p. 418): this was documented by *Araeoscelis* from the Lower Permian. In his classification Williston (1917, p. 420) included the Theromorpha, Therapsida, Sauropterygia and Placodontia in the Synapsida, whereas he coined the term Parapsida for a division including the Ichthyosauria, Squamata and Protorosauria (including the Araeoscelidia and Acrosauria).

In 1925, Williston removed the Sauropterygia (Nothosauria and Plesiosauria) and Placodontia from the Synapsida because of the different relation of the single temporal opening to the postorbital and squamosal bones, and included them in a separate subclass. He resurrected Baur's (1887, p. 93) old term Synaptosauria to designate the latter, 'indicating a rather wistful hope that some relationship to mammal-like forms might be proved' (Romer 1956, p. 652). The Parapsida continued to exist as a polyphyletic assemblage, including forms as diverse as *Mesosaurus*, ichthyosaurs, *Araeoscelis*, *Protorosaurus*, *Saphaeosaurus* and squamates.

The situation proved unsatisfactory, particularly after the description of *Prolacerta* by Parrington (1935), a diapsid reptile with an incomplete lower temporal arcade. The fossil was interpreted as a lizard precursor, and thus refuted Williston's (1914) assumptions about the history of the lizard skull. The Squamata were recognized as diapsid reptiles, the temporal region of the skull having been opened up by the reduction and eventual loss of the lower temporal arcade rather than by emargination from below.

Romer (1968, p. 113) relates how it was generally acknowledged that Williston (1925) had correctly grouped together the Sauropterygia and placodonts on the basis of the single upper temporal opening, and how E. H. Colbert, 'after discussion with me and others, reasonably suggested Euryapsida as a substitute' for the 'awkward' term Synaptosauria (Colbert 1955). *Araeoscelis* was included within the Euryapsida as their earliest representative on the basis of the upper temporal fenestra, the position of which was confirmed by Vaughn (1955). On that basis, Romer developed the concept of an early radiation of euryapsids, poorly represented in the Palaeozoic fossil record as opposed to the Mesozoic record, including sauropterygians and placodonts.

The concept of the Euryapsida as conceived by Romer stands in sharp contrast to the hypothesis of a diapsid relation of sauropterygians. A diapsid relationship of nothosaurs was first proposed by Jaekel (1910, pp. 327–328). He based his suggestion mainly on the configuration of the upper temporal arcade of *Anarosaurus*, which he found to resemble the upper temporal arcade of diapsid reptiles. Jaekel also noted a posterior projection at the hind end of the maxilla in *Simosaurus*, which he compared to the posterior projection of the jugal in a lizard with a reduced lower temporal arcade, and he also reconstructed such a projection in the skull of *Anarosaurus*. The latter point was not confirmed by the reconstruction of the skull of *Anarosaurus* by Carroll (1981, fig. 32), however. The diapsid relations of nothosaurs were further supported by Kuhn-Schnyder (1967, 1980) who based his arguments on a reinvestigation of the skull of *Simosaurus*. He believed the shape of the jugal bone to be best explained by the loss of the lower temporal arcade in a diapsid reptile, rather than by ventral emargination of the cheek region, a view rejected by Romer (1968). In 1981, Carroll described *Claudiosaurus* from the Upper Permian of Madagascar, a genus that he designated as a possible plesiosaur ancestor. The comparison of *Claudiosaurus* to *Anarosaurus* and *Youngina* once again asserted the similarity shared by sauropterygians and diapsids in the pattern of skull structure. Carroll (1981) emphasized the wide open cheek and the narrowness of the upper temporal arcade in *Claudiosaurus* and sauropterygians, features that were judged to be closely comparable to the pattern observed in the 'eosuchian' genus *Youngina*. Currie (1981, p. 164) briefly commented on the diapsid relationships of *Claudiosaurus* (and implicitly of sauropterygians), emphasizing the loss of a contact between parietal and postorbital in younginiforms and in *Claudiosaurus*. In his cladistic analysis of diapsid reptiles, Benton (1985) found *Claudiosaurus* to share all diapsid and most neodiapsid synapomorphies, concluding that *Claudiosaurus* is best placed within the Diapsida, as the plesiomorphic sister group of the Neodiapsida. Sues (1987*a*) finally envisaged the possibility that the similarities shared by *Claudiosaurus* and sauropterygians might be convergent, but he concluded that irrespective of the placement of the latter genus, the Sauropterygia would have to be included within the Lepidosauromorpha, one of the two major subgroups of Benton's (1985) Neodiapsida.

This brief literature review documents the emergence of a general concensus concerning the diapsid relationships of the Sauropterygia. From the analysis of Sues (1987*a*) it follows, however, that the alleged sister-group relationship (or ancestor–descendant relationship (Carroll 1981)) of *Claudiosaurus* and sauropterygians might well bear closer scrutiny. By implication, the diapsid relations of sauropterygians thereby come under reconsideration because Carroll (1981) used *Claudiosaurus* to substantiate this hypothesis of grouping. The discussion of sauropterygian relationships will proceed from two alternative perspectives, involving the analysis of pattern first, followed by a discussion of process.

Pattern analysis

The Sauropterygia traditionally include nothosaurs and plesiosaurs (Romer 1966). The monophyly of the Sauropterygia is well corroborated by several synapomorphies (Sues 1987*a*). Carroll & Gaskill (1985, p. 344) have identified the reversed relationship of scapula and clavicle as one of the several diagnostic features: 'In contrast to the vast majority of tetrapods, the scapulae lie superficial to the clavicles'. Other synapomorphies of the Sauropterygia include the absence of postparietals and tabulars, the closure of the bony palate by an expansion of the pterygoids that completely cover the basicranium, the absence of the posterior stem on the interclavicle (developed in *Simosaurus* according to Sues (1987*a*, p. 127)) and the loss of the pisiform. A corresponding element in the carpus of *Dactylosaurus schroederi* is more parsimoniously interpreted as a neomorph (Sues & Carroll 1985, p. 1607).

The nothosaurs were subdivided by Peyer (1934) into two families, the Pachypleurosauridae and the Nothosauridae. Of these, only the Pachypleurosauridae can claim monophyletic status (see below). The Nothosauridae *sensu* Peyer (1934) have been shown to be a paraphyletic assemblage by Sues (1987*a*). The pattern analysis presented below will therefore include the Pachypleurosauridae as opposed to all other, 'non-pachypleurosaur sauropterygians' as terminal taxa. That all 'non-pachypleurosaur sauropterygians' form a monophyletic taxon in their turn is documented by several shared derived characters (Sues 1987*a*), among which the enlargement of the upper temporal fossae and the increase in the number of sacral ribs (five or six pairs being present) figure prominently.

Because of the hypotheses put forward in the literature reviewed above, the relationships of these taxa will be tested against several fossil taxa currently included within the Diapsida, Neodiapsida and Lepidosauromorpha. The outgroup of the Diapsida is represented by the genus *Paleothyris* (Carroll 1969*a*). The diapsid sister group of the Neodiapsida is represented by *Petrolacosaurus* (Reisz 1981). To test the hypothesis of the Synaptosauria, *Araeoscelis* is also included in the analysis. This genus is currently classified together with *Petrolacosaurus* within the Araeoscelidia (Reisz *et al.* 1984; Benton 1985). The genera *Coelurosauravus* (Carroll 1978; Evans 1982; Evans & Haubold 1987) and *Claudiosaurus* (Carroll 1981) are included to represent an extended range of diapsid morphology. The genera *Youngina* and *Gephyrosaurus* (Evans 1980, 1981) are included as representatives of lepidosauromorph neodiapsids.

The Archosauromorpha are excluded from the analysis of sauropterygian relationships because the two groups share none of the synapomorphies listed by Benton (1985). One surprising feature in the description of pachypleurosaurs (see above) and of *Pistosaurus* (Sues 1987*a*) is the presence of a free anterior process on cervical ribs, otherwise thought to represent an archosauromorph feature (Evans 1984, 1988; Benton 1985). However, a considerable degree of incongruence must be admitted for this character (Rieppel 1987*b*) which might in fact characterize a more inclusive group, as it is also observed in *Araeoscelis*, *Petrolacosaurus* (Reisz *et al.* 1984, p. 65, character 5; see also Reisz 1981, p. 37) as well as in the ichthyosaur *Mixosaurus* (personal observation).

Evans (1986) has recently reviewed archosauromorph braincase structure in a search for useful synapomorphies characterizing the group or some of its subgroups. In this work she recognized an interesting pattern of ossification of the base of the pila antotica. In captorhinomorph reptiles, the base of the pila ossifies as the clinoid process of the basisphenoid; this is the plesiomorph condition that is essentially retained in lepidosauromorphs, although a contribution of the prootic is possible in the latter group. In early archosauromorphs, on the other hand, the clinoid process ossifies as part of the prootic, whereas in later archosaurs the pila antotica gives rise to the pleurosphenoid ossification incorporated into the lateral wall of the braincase. No complete braincase of any pachypleurosaur is known, but acid-prepared specimens of *Simosaurus* permit the study of the complete braincase (Huene 1952). This genus retains the plesiomorph condition, i.e. a clinoid process that is entirely part of the basisphenoid ossification (personal observation).

Analysis of the interrelationships of the terminal taxa enumerated above is tested on the basis of characters used by Gauthier (1984), Benton (1985) and Evans (1984, 1988) to characterize successively less-inclusive levels in the hierarchy of diapsid classification. Cladistic analysis of the distribution of the characters involved in the study and their most parsimonious interpretation was done by using MacClade version 2.1, written by Wayne Maddison and David Maddison. The characters used in the classification of diapsid reptiles are defined as follows.

Characters of the Diapsida

1. Temporal fenestration. The diagnosis of the Diapsida is currently based on the presence of an upper temporal fossa only to permit the inclusion of the genus *Araeoscelis* into that group on account of several synapomorphies derived from the postcranial skeleton and shared with the earliest fully diapsid reptile, *Petrolacosaurus* (Reisz 1981). On this diagnosis, however, the hypothesis of the Synaptosauria is defined away. With no assumptions made concerning the mode of temporal fenestration (by emargination or by the loss of a lower temporal arcade) it might be argued that a single (upper) temporal opening is more widely distributed and thus characterizes a more inclusive group, i.e. the Synaptosauria, as opposed to the presence of two temporal fenestrae which characterize the Diapsida, a subgroup of the Synaptosauria. For that reason, two different approaches to temporal fenestration were used for the cladistic analysis. A multistate character approach differentiated between the presence of no (*Palaeothyris*), one (*Araeoscelis*, Sauropterygia), and two (all other genera included) temporal fenestrae. A binary approach differentiated between the absence (*Paleothyris*) and presence (all other genera) of an upper temporal fossa. Both approaches yielded the same most parsimonious solution. It is therefore concluded that the Diapsida may indeed be diagnosed by the presence of an upper temporal fossa.

The anterolateral margin of the diapsid upper temporal fenestra is formed by a triradiate postorbital; posteriorly, the upper temporal fossa is closed by a triradiate or tetraradiate squamosal (Evans 1988). The triradiate postorbital was not coded as a separate character because it is correlated with the formation of an upper temporal fenestra. Its absence in non-pachypleurosaur Sauropterygia is correlated with the enlarged upper temporal fossa.

2. Presence of a suborbital fenestra (inferior orbital foramen *sensu* Oelrich (1956)). The modification of the maxilla, palatine, ectopterygoid and jugal as a result of the formation of a suborbital fenestra (Reisz 1981) is listed as a separate character complex by Benton (1985), a practice not adopted here because of character correlation. Sues (1987*a*) used the absence of the contact between ectopterygoid and maxilla as an argument for the inclusion of the Sauropterygia into the Diapsida. In fact, the ectopterygoid is lacking in all well-preserved pachypleurosaurids, although it retains its contact with the maxilla in those non-pachypleurosaurid sauropterygians that retain the bone.

3. This is the reason why presence as opposed to absence of the ectopterygoid was introduced as a separate character into the cladistic analysis. Note that the presence of an ectopterygoid in *Paleothyris* (and other captorhinomorphs) is equivocal.

4. Presence of large posttemporal fenestrae. The specification of size is emphasized with respect to this character state in the present context. The presence of large posttemporal fenestrae, bordered by a narrow occipital flange of the squamosal, the small tabular, the supraoccipital and a well-developed paroccipital process was used as a diapsid synapomorphy by Reisz (1981, p. 63), who emphasized that the occiput of primitive captorhinomorphs such as *Paleothyris* is poorly known, but may well have incorporated a small posttemporal fenestra (Carroll 1969*a*). The posttemporal fenestra is small in *Araeoscelis*, pachypleurosaurids and some non-pachypleurosaur sauropterygians.

Characters of the Neodiapsida (sensu Benton 1985)

5. Reduction of the lacrimal bone. The Neodiapsida are characterized by the failure of the lacrimal bone to enter the external naris. In all well-preserved pachypleurosaurids, the lacrimal is absent; its presence is questionable in those non-pachypleurosaur sauropterygians for which the bone has been described. The configuration of the lacrimal bone was thus considered as a multistate character, involving its reduction and its total loss.

6. A descending flange of the parietal bone forms the medial margin of the upper temporal fossa, providing a site of origin for the jaw adductor musculature.

7. The Neodiapsida bear no caniniform teeth on the maxilla. Some non-pachypleurosaur 'nothosaurs' bear one or two enlarged teeth on the preorbital portion of the maxilla, preceded by a few distinctly smaller maxillary teeth.

8. The lateral exposure of the quadrate bone is correlated with the reduction of the quadratojugal and squamosal. These features were coded separately by Benton (1985, characters B_4 and B_5), a practice not adopted in the present analysis. The character is difficult to determine in the Pachypleurosauridae. *Claudiosaurus* is coded as plesiomorphous with respect to this feature by Benton (1985); *Serpianosaurus*, as described above, has the quadrate no more exposed in lateral view than the latter genus. It retains a vertically orientated quadratojugal, which forms an extended sutural contact with a large ventral process of the squamosal covering the quadrate laterally. The quadrate is also concealed in lateral view in non-pachypleurosaur sauropterygians.

9. The Neodiapsida are characterized by a posterior excavation of the quadrate bone, which results in a concavity permitting the suspension of a tympanic membrane.

10. The Neodiapsida are characterized by the presence of a slender stapes, correlated with the hypothesized presence of a tympanic membrane and providing an impedance-matching sound transmitting system. Carroll & Gaskill (1985, fig. 14*g*) postulated the presence of a slender stapes in one specimen of *Neusticosaurus*, but the interpretation of the fossil must remain equivocal. Because of the hypothesized presence of a relatively large tympanic membrane, the assumption of the presence of a slender stapes seems reasonably safe. The presence of a slender stapes remains questionable in non-pachypleurosaur sauropterygians, which seem to have lacked a tympanic membrane.

11. The Neodiapsida are characterized by the absence of teeth on the parasphenoid. Benton (1985) adds the absence of teeth on the pterygoid as another neodiapsid feature, but this character is omitted from the present analysis because of its highly incongruent distribution.

12. The Neodiapsida are characterized by the presence of a retroarticular process, a feature usually considered to be related to the function of the depressor mandibulae muscle (Gans 1966). On the other hand, the character may also be correlated with the development of an impedance-matching middle ear because it may serve the suspension of a relatively large tympanic membrane as in modern lizards. In pachypleurosaurs, however, the lower edge of the tympanic membrane is supported by a posterior projection of the mandibular condyle of the quadrate which fits into a groove in the dorsal surface of the retroarticular process upon jaw opening.

13. The Neodiapsida are characterized by the absence of an ossified olecranon on the ulna. The character is discussed by Benton (1985, p. 112, character B_{11}).

14. The acetabulum of neodiapsids is rounded, rather than elongate.

15. The femur of the Neodiapsida is slender and sigmoidally curved, rather than massive and straight. It is interesting to note that *Araeoscelis* shows a neodiapsid femur, whereas sauropterygians do not: the character may be correlated with habitus and mode of life. Benton (1985, character B_{15}) included the size relation between femur and humerus in his list of neodiapsid features. In all well-known pachypleurosaurids, but also in *Ceresiosaurus* and perhaps other non-pachypleurosaurid sauropterygians, the relative size of the humerus is dependent on age and sex of the individual. The character is therefore omitted from the present analysis.

16. In the Neodiapsida, the distal articulations of the femur for tibia and fibula are in the same level.

Characters of the Lepidosauromorpha (*sensu Benton* 1985)

17. In the Lepidosauromorpha, the postfrontal enters the upper temporal fossa rather than being excluded from it by a contact of the postorbital with the parietal.

18. The Lepidosauromorpha are claimed to be characterized by the presence of accessory intervertebral articulations (zygosphene–zygantrum system). This is one of the more important features that has been used to link sauropterygians to lepidosauromorph diapsids (Sues 1987*a*). However, problems of homology of intervertebral articulations are involved, as is outlined in the morphological description given above (see also Hoffstetter & Gasc 1969). Some pachypleurosaurs show dorsal and ventral intervertebral articulations (Carroll & Gaskill 1985, p. 369); and morphological description above) which may not be homologous with the accessory intervertebral articulations in lepidosauromorphs. Evans (1988, and personal communication) restricts the occurrence of a zygosphene–zygantrum system to the Lepidosauria proper, considering the interspinous joints of younginiforms as non-homologous. Placodonts show only ventral (hyposphene–hypantrum) articulations (Sues 1987*b*) which they share with some dinosaurs (Romer 1956, p. 226; Hoffstetter & Gasc 1969, p. 207). The character is retained in the following test of sauropterygian relationships, but parsimony analysis only highlights problems of homology in the interpretation of accessory intervertebral articulations.

19. The dorsal ribs of the Lepidosauromorpha are holocephalous. *Coelurosauravus* is described as retaining dichocephalous ribs in the anterior trunk region (Evans 1982, p. 106; see also Evans & Haubold 1987); the cervical and the posterior dorsal ribs are holocephalous. *Coelurosauravus* was therefore coded as being polymorphic for this character.

Benton (1985, characters R_3, R_5, R_6) used additional features to characterize the

Lepidosauromorpha that are omitted from the present analysis. The relative length of the cervical vertebrae must be judged in conjunction with the number of elements included in the neck. As sauropterygians have a tendency to increase the number of cervical vertebrae, it is difficult to use the character for meaningful comparison with other lepidosauromorphs. The co-ossification of sternal plates and their relation to dorsal ribs is known only in some aquatic younginiforms (Currie 1981, 1982) and therefore cannot add to the analysis of sauropterygian interrelationships.

On the basis of the above discussion, the following data matrix (see table 3) obtains:

1. temporal fossae: none (0); one (1); two (2);
2. suborbital fenestra: absent (0); present (1);
3. ectopterygoid: present (0); absent (1);
4. posttemporal fossae: small (0); large (1);
5. lacrimal: enters external naris (0); reduced (1); absent (2);
6. lateral parietal flanges: absent (0); present (1);
7. caniniform teeth on maxilla: present (0); absent (1);
8. quadrate: not exposed laterally (0); exposed laterally (1);
9. quadrate: not excavated posteriorly (0); concave posteriorly (1);
10. stapes: massive (0); slender (1);
11. parasphenoid teeth: present (0); absent (1);
12. retroarticular process: absent (0); present (1);
13. olecranon on ulna: present (0); absent (1);
14. acetabulum: elongate (0); rounded (1);
15. femur: massive, straight (0); slender, sigmoidal (1);
16. distal articular surfaces on femur (0): uneven; level (1);
17. postfrontal enters upper temporal fossa: no (0); yes (1);
18. accessory intervertebral articulations: absent (0); present (1);
19. dorsal ribs: double headed (0); single headed (1).

The most parsimonious cladogram (figure 12) obtained on the basis of the data matrix given in table 3 refutes the concept of the Synaptosauria. *Araeoscelis* is included within the Diapsida, the group being diagnosed by the presence of a single upper temporal fenestra. *Araeoscelis* was classified as the sister group of *Petrolacosaurus* by Reisz *et al.* (1984) on the basis of a number of

TABLE 3. DATA MATRIX FOR THE TAXA INCLUDED IN THE CLADISTIC ANALYSIS

(The characters are defined in the text.)

taxa	characters	1				5					10					15				19
Paleothyris		0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Araeoscelis		1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	?
Petrolacosaurus		2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coelurosauravus		2	1	0	1	1	0	1	0	0	?	?	0	0	?	1	1	1	0	0
and																				1
Claudiosaurus		2	1	0	1	1	1	1	0	0	?	0	0	1	?	1	1	?	0	1
Youngina		2	1	0	1	1	0	1	1	1	1	1	?	1	1	1	1	1	0	?
Gephyrosaurus		2	1	0	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1
Pachypleurosauridae		1	0	1	0	2	0	1	0	1	1	1	1	1	0	0	1	1	1	1
non-pachypleurosaur																				
Sauropterygia		1	0	0	0	1	1	1	0	0	?	1	0	1	0	0	1	1	1	1
and					1	2							1							

shared derived characters in the postcranial skeleton; this arrangement implies convergence of the structure of the femur in *Araeoscelis* and neodiapsids (*sensu* Benton 1985), probably correlated with the agile terrestrial habitus. The Pachypleurosauriae and the non-pachypleurosaur sauropterygians form a monophyletic taxon, the Sauropterygia, inserted between the lepidosauromorph genera *Youngina* plus *Gephyrosaurus* on the one hand and *Claudiosaurus* on the other. The hierarchy of synapomorphies is as follows (see also figure 12).

A. Diapsida
  A_1. upper temporal fossa present.
  A_2. Suborbital fenestra present (absent in sauropterygians with the exception of *Pliosaurus*).
  A_3. Posttemporal fenestra present, enlarged compared with *Paleothyris* (reversals in *Araeoscelis* and sauropterygians).
B.
  B_1. Slender femur, sigmoidally curved.
C. (Neodiapsida *sensu* Benton (1985))
  C_1. Slender femur, sigmoidally curved (modified in sauropterygians).
  C_2. Lacrimal bone does not enter external naris, or is lost.
  C_3. Caniniform teeth on maxilla absent.
  C_4. Distal articulations on femur are level.
  C_5. Postfrontal enters upper temporal fossa (reversal in all Archosauromorpha).
D.
  D_1. No olecranon on ulna.
  D_2. Dorsal ribs single headed.
E.
  E_1. Quadrate excavated posteriorly (reversal in non-pachypleurosaur sauropterygians).
  E_2. Slender stapes
  E_3. Parasphenoid teeth absent (convergence in *Araeoscelis*).
  E_4. Retroarticular process present (absent in some non-pachypleurosaur sauropterygians).
F. Neodiapsida
  F_1. Quadrate laterally exposed.
  F_2. Acetabulum rounded.
G.
  G_1. Suborbital fenestra absent (reversal in *Pliosaurus*).
H.
  H_1. Ectopterygoid absent.

This list of synapomorphies raises several questions concerning the classification of the Sauropterygia. There can be no doubt that the Sauropterygia are to be included within the Neodiapsida, but the selection of the node of the cladogram which is to define the Neodiapsida is largely an arbitrary matter (see Rieppel (1987*c*) for a discussion of theoretical issues). Benton (1985) places the dividing point further down along the axis of the cladogram than does Evans (1988). A possible suggestion is to define the Neodiapsida by the presence of an impedance-matching middle ear as is indicated by a posteriorly excavated quadrate.

Sues (1987*a*) included the Sauropterygia within the Lepidosauromorpha on the basis of

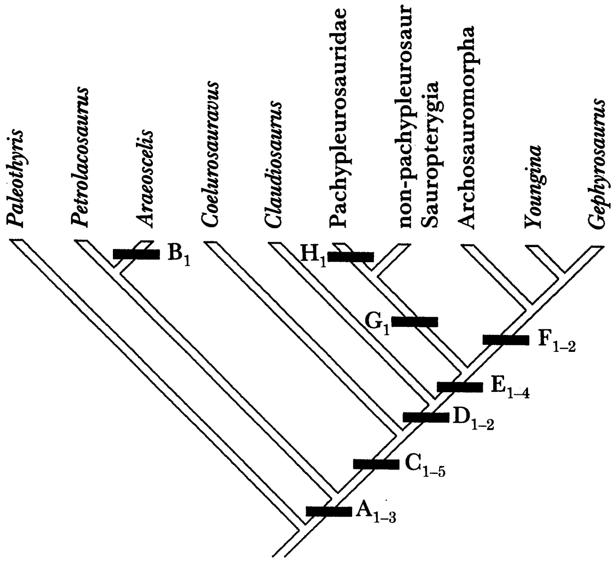

FIGURE 12. A cladogram of sauropterygian interrelationships (for further explanation see text).

Benton's (1985) synapomorphy scheme. This classification is here considered as not sufficiently supported by undisputed synapomorphies. The postfrontal enters the upper temporal fossa in *Coelurosauravus* and *Claudiosaurus*. For intervertebral articulations, details of structure and parsimony analysis preclude unequivocal statements of homology (see comments on the classification of placodonts below). Holocephalous dorsal ribs are also observed in *Claudiosaurus* and in the cervical and posterior dorsal region of *Coelurosauravus* (Evans 1982; Evans & Haubold 1987). The other lepidosauromorph features recognized by Benton (1985, pp. 136–138) have been discussed above.

The position of the Sauropterygia with respect to the archosauromorph–lepidosauromorph dichotomy was tested by the inclusion of the Archosauromorpha in the parsimony analysis. The latter clade was coded O for characters 17–19 (lepidosauromorph characters *sensu* Benton (1985)). The result was unambiguous: whereas the placement of *Youngina* with respect to the Archosauromorpha on the one hand and to *Gephyrosaurus* on the other was equivocal (unresolved trichotomy), the Sauropterygia were most parsimoniously placed outside the archosauromorph–lepidosauromorph dichotomy. Shifting the archosauromorph clade down along the axis (lower edge) of the cladogram progressively increased the number of steps implied. For these reasons, the Sauropterygia are inserted into the Neodiapsida outside the archosauromorph–lepidosauromorph dichotomy.

The relations of the Placodontia

Kuhn-Schnyder (1980, p. 163) rejected any relation of placodonts with sauropterygians, in contradiction to Romer (1956, 1968, p. 116). He was forced to do so because he believed sauropterygians are of diapsid origin, whereas placodonts show a jugal and quadratojugal still in contact below the upper temporal fossa, i.e. the primitive anapsid condition (see Sues (1987*b*) for a description of the skull of *Placodus*). The interrelationships of the Placodontia were considered unresolved by Carroll (1981, p. 377) because they do not fit into the diapsid relations of *Claudiosaurus* and its alleged descendants, the Sauropterygia. However, these denials of sauropterygian relationships of the Placodontia either imply assumptions about unknown processes concerning the mode of temporal fenestration, or they depend on arguments based on overall similarity.

Sues (1987*b*), on the other hand, has argued that placodonts can be linked to the Diapsida on the basis of several features, but he again questioned any sauropterygian relationships. However, one of the salient features diagnosing the Sauropterygia (nothosaurs plus plesiosaurs) is the inverse relation of the dermal to the endochondral pectoral girdle elements (Carroll & Gaskill 1985, p. 344). The same relation of the two elements is described and figured by Drevermann (1933, p. 349 and fig. 75*b*) for *Placodus gigas*. Drevermann (1933, p. 349) emphasized that scapula and clavicle were found in association, with the scapula showing a rugous facet on the anterodorsal part of its medial surface which received the ascending wing of the clavicle. This character might indicate some relationship with 'nothosaurs' and plesiosaurs. In spite of Drevermann's assertion concerning the association of the elements in *Placodus*, H.-D. Sues (personal communication) considers the structure of the pectoral girdle in placodonts as still open to question.

To test the relations of *Placodus*, the genus was added to the genera included into the data matrix given in table 3. The data were analysed with and without inclusion of the inversed relations of clavicle and scapula to the list of characters. In either case, *Placodus* was most parsimoniously placed as the sister taxon of the Sauropterygia (figure 13). If this placement of the Placodontia is accepted, the group may be included together with the Sauropterygia within a monophyletic taxon of higher rank, the Euryapsida, this being subordinated to the Diapsida and Neodiapsida respectively.

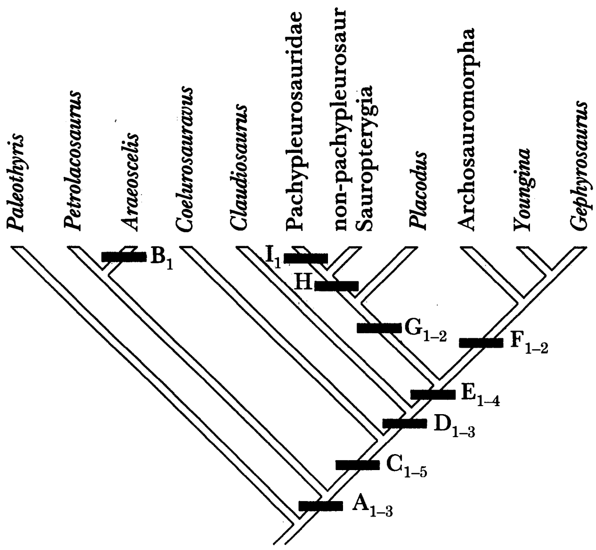

FIGURE 13. A cladogram of euryapsidan interrelationships (for further explanation see text).

To test the position of the Euryapsida with respect to the archosauromorph–lepidosauromorph dichotomy, the Archosauromorpha were again added to the list of taxa examined. The latter clade was coded O for characters 17 and 19, whereas character 18 was coded as polymorphic (the hyposphene–hypantrum articulation is shared by placodonts and dinosaurs). The result was the same as in the test of the sauropterygian relations: whereas the placement of *Youngina* with respect to the Archosauromorpha on the one hand and to *Gephyrosaurus* on the other continues to be equivocal (unresolved trichotomy), the Euryapsida were most parsimoniously placed outside the archosauromorph–lepidosauromorph dichotomy. Shifting the archosauromorph clade down along the axis (lower edge) of the cladogram progressively increased the number of steps implied.

The synapomorphies specifying the nodes in the cladogram reproduced in figure 13 are the following.

A. Diapsida
- A_1. Upper temporal fossa present.
- A_2. Suborbital fenestra present (absent in sauropterygians with the exception of *Pliosaurus*).
- A_3. Posttemporal fenestra present, enlarged compared with *Paleothyris* (reversals in *Araeoscelis*, in sauropterygians and in placodonts).

B.
- B_1. Slender femur, sigmoidally curved.

C. (Neodiapsida *sensu* Benton (1985))
- C_1. Slender femur, sigmoidally curved (modified in sauropterygians plus placodonts).
- C_2. Lacrimal bone does not enter external naris, or is lost.
- C_3. Caniniform teeth on maxilla absent.
- C_4. Distal articulations on femur are in level.
- C_5. Postfrontal enters upper temporal fossa (reversal in all Archosauromorpha).

D.
- D_1. No olecranon on ulna.
- D_2. Dorsal ribs single headed.
- D_3. Presence of lateral parietal flanges (absent in pachypleurosaurs and in *Youngina*).

E. Neodiapsida
- E_1. Quadrate excavated posteriorly (reversal in non-pachypleurosaur sauropterygians).
- E_2. Slender stapes.
- E_3. Parasphenoid teeth absent (convergence in *Araeoscelis*).
- E_4. Retroarticular process present (absent in some non-pachypleurosaur sauropterygians).

F.
- F_1. Quadrate laterally exposed.
- F_2. Acetabulum rounded.

G. Euryapsida
- G_1. Inversed relation of clavicle and scapula.
- G_2. Suborbital fenestra absent (reversal in *Pliosaurus*).

H. Sauropterygia
- H_1. The monophyly of the Sauropterygia is discussed by Sues (1987*a*). Sauropterygians differ from placodonts in the structure of the palate: in the first group, the pterygoids (rather than the palatines) expand to close the palate, completely covering the base of the braincase.

I.
- I_1. Ectopterygoid absent.

The inclusion of *Placodus* into the analysis results in a change of the level of inclusiveness at which some characters form groups. For instance, the intervertebral articulations of sauropterygians comprise a dorsal and a ventral component, a system that must have been developed independently from the zygosphene–zygantrum articulation observed in lepidosaurs. In *Placodus*, a ventral intervertebral articulation (hyposphene–hypantrum articulation (Drevermann 1933, pp. 340–341; Sues 1987*b*, p. 143)) is described which is shared with some dinosaurs (archosaurs). Accessory intervertebral articulations do not seem to provide a sound basis for the placement of euryapsids in relation to other diapsids.

The Euryapsida are defined in the above synapomorphy scheme on the inverse relation of clavicle and scapula, and on the absence of a suborbital fenestra (implying reversal in *Pliosaurus* (Andrews 1913, vol. 2, text-fig. 1)). Sues (1987*b*) described structures possibly homologous with suborbital fenestrae in the skull of *Placodus*. To account for this conjecture of similarity, the classification of *Placodus* was tested with the suborbital fenestrae coded alternatively as being present or absent. Either strategy did not alter the most parsimonious placement of *Placodus* as sister group of the Sauropterygia. However, considering the structure of the pectoral girdle as unsettled, and the suborbital fenestrae as being present in *Placodus*, the characterization of the Euryapsida as given above is thrown into doubt. The group might still be defined on the small posttemporal fenestrae (these are large in *Claudiosaurus* and polymorphic in non-pachypleurosaur sauropterygians) and on the absence of the lacrimal bone (present in *Claudiosaurus* and in some non-pachypleurosaur sauropterygians).

Process analysis

The classification of *Araeoscelis* with *Petrolacosaurus* within the Araeoscelidia (Reisz *et al.* 1984; Benton 1985) implies character reversal in the temporal fenestration of the diapsid skull. It must either be assumed that the lower temporal fossa was developed independently in *Petrolacosaurus* and all other diapsids that share it, or the ventral cheek region in *Araeoscelis* became closed secondarily (Carroll 1981), perhaps in adaptation to durophagous habits (Reisz *et al.* 1984). A similar point can be made for the Sauropterygia if the Placodontia are admitted to represent their sister group and thus diapsid derivatives: either the latter group has secondarily closed the lower temporal region (Sues 1987*b*), or its opening was acquired independently in the Sauropterygia.

Two mechanisms of reduction of the dermatocranium covering the temporal region of the skull have been identified in reptiles. The first mechanism is emargination as exemplified by some turtles (Romer 1956; Kilias 1957), the second is temporal fenestration. The cheek region of diapsid reptiles may show further reduction by the loss of the lower temporal arcade (the upper temporal arcade is lost in some lizards, amphisbaenians and in snakes). The reduction of the lower temporal region of the dermatocranium permits the expansion of the jaw adductor musculature on to the lateral surface of the lower jaw, and is prerequisite for the development of streptostyly in diapsids (Rieppel & Gronowski 1981). On the other hand, the reduction of the lower temporal region causes no functional problems: it is not a skull region with particular supporting function resisting forces that result from jaw action in *Petrolacosaurus* (Reisz 1981, p. 25), nor can this area of the dermatocranium give rise to jaw adductor muscle fibres. With an origin deep down on the cheek, the fibre length would severely restrict gape (Rieppel & Gronowski 1981). The claim that the lower temporal region in *Araeoscelis* and *Placodus* was secondarily closed in adaptation to durophagous habits still awaits support by biomechanical analysis. Instead, it might appear more advantageous to open up the cheek region in adaptation to durophagy, as this permits the expansion of the jaw adductor musculature and hence increases the adductive force exerted on the lower jaw. That the once reduced lower temporal arcade is redeveloped secondarily has been postulated for *Sphenodon* (Whiteside 1986; see below), but this seems to be correlated with the immobilization of the quadrate to permit translational movements of the jaws (Robinson 1976) rather than with durophagy. In that sense, *Sphenodon* does not lend support to the hypothesis that the lower cheek region is secondarily closed in *Araeoscelis* and placodonts.

The loss of the lower temporal arcade, as opposed to ventral emargination, was recognized as a pattern of reduction of the dermatocranium in diapsid reptiles after the discovery and description of the fossil genus *Prolacerta* from the Lower Triassic of South Africa by Parrington (1935). In this diapsid reptile, the posterior process of the jugal no longer meets the quadratojugal. As is implied in its name, the animal was interpreted to document the diapsid origin of lizards, providing an intermediate stage of reduction. It is currently classifed as a member of the archosauromorph Prolacertiformes (Evans 1984, 1987; Benton 1985).

Since the time of the description of *Prolacerta*, a great variety of early diapsids from the Upper Permian and Triassic have come to light which are characterized by an incomplete lower temporal arcade. The taxa in question include the prolacertimorph genera *Protorosaurus* (Seeley 1888), *Prolacerta* (Parrington 1935), *Kadimakara* (Bartholomai 1979), *Macrocnemus* (Kuhn–Schnyder 1962), *Malerisaurus* (Chatterjee 1986), *Tanystropheus* (Wild 1973), and *Tanytrachelos* (Olsen 1979); the pleurosaur genera *Palaeopleurosaurus* and *Pleurosaurus* (Carroll 1985); the sphenodontids *Clevosaurus* (Robinson 1973), *Gephyrosaurus* (Evans 1980), *Planocephalosaurus* (Fraser 1982) and *Diphydontosaurus* (Whiteside 1986); the flying reptiles *Coelurosauravus* (Evans 1982; Evans & Haubold 1987), *Kuehneosaurus* (Robinson 1962) and *Icarosaurus* (Colbert 1966, 1970); and the thalattosaur genera *Askeptosaurus* (Kuhn-Schnyder 1952), *Clarazia*, *Hescheleria* (Rieppel 1987*b*) and *Thalattosaurus* (Merriam 1905). Carroll (1985, p. 26) classified the Pleurosauridae with the Sphenodontidae within the Sphenodontia, and on the basis of fossil evidence concluded that the incomplete lower temporal arcade may well represent the plesiomorph condition within the group. This conclusion is corroborated by the application of cladistic techniques (Whiteside 1986) implying that the complete lower temporal arcade and the resulting monimostyly of the quadrate is secondary in those sphenodontids where it occurs.

The loss of the upper temporal arcade in extant diapsid reptiles appears to be the result from paedomorphosis (Rieppel 1984), and there is no reason to evoke a different mechanism for fossil taxa. The loss of the lower temporal arcade may be due to the same mechanism.

All of the diapsid genera mentioned above share a similar triradiate structure of the jugal bone (figure 14). There is an anterior (maxillary) process lining the posteroventral margin of the orbit. A dorsal process rises up behind the orbit to meet the postorbital. Finally, there is a posterior ventral process of variable length which in the plesiomorph diapsid condition (*Petrolacosaurus*, *Youngina*) meets the anterior process of the quadratojugal below the lower temporal fossa (rather than behind as in *Sphenodon*). The loss of the lower temporal bar appears to result from the reduction of the anterior ramus of the quadratojugal and of the posterior ramus of the jugal.

Ontogenetic data on *Sphenodon* suggest that the posterior ramus of the jugal ossifies in a craniocaudal direction (Howes & Swinnerton 1901, stage R; see also figure 14*a*). Reduction

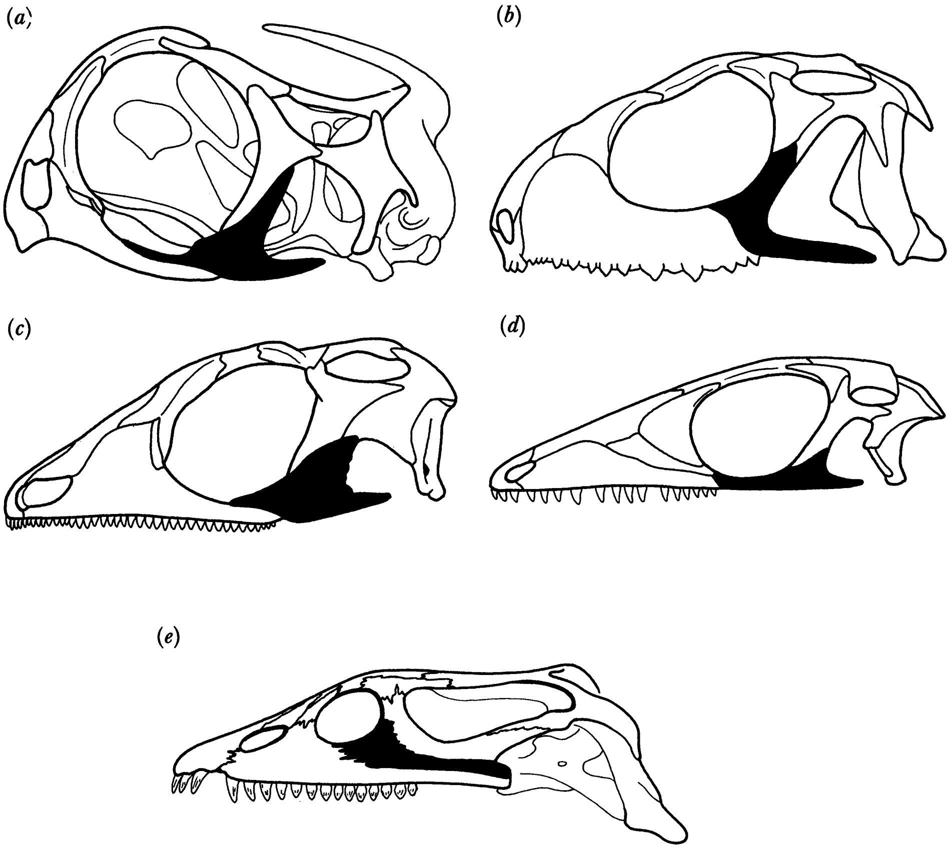

FIGURE 14. The shape of the jugal bone in diapsid reptiles as compared to Simosaurus. (*a*) *Sphenodon punctatus*, embryo (after Howes & Swinnerton 1901, plate 3, fig. 10); (*b*) *Clevosaurus* (after Robinson 1973, fig. 4); (*c*) *Gephyrosaurus* (after Evans 1980, fig. 1); (*d*) *Prolacerta* (after Robinson 1973, fig. 4); (*e*) *Simosaurus* (original).

by paedomorphosis would thus result in a jugal carrying a posterior ramus of variable length: this is the shape of the jugal observed in the early diapsids mentioned above, which show a variable degree of incompleteness of the lower temporal arcade. In the case of the sphenodontid *Diphydontosaurus* it has even been observed that the lower temporal arcade may be complete in old animals (Whiteside 1986, p. 393; but see further comments below). In the case of complete reduction, one would expect a posteriorly angulated jugal as is observed in *Claudiosaurus* (Carroll 1981).

This is not the pattern observed in sauropterygians, however. Here, the jugal is either evenly curved, as in pachypleurosaurids (comparable to ichthyosaurs and some advanced lizards), or it appears truncated posteriorly, as in non-pachypleurosaurid 'nothosaurs'. *Simosaurus* carries a short posterior projection of the jugal, recognized by Jaekel (1910) now broken off in the Crailsheim specimen (see Kuhn-Schnyder 1961) but not in other material. In *Simosaurus*, the jugal does not form a pointed and free-ending posterior process as it does in typical diapsids; instead, the jugal is underlain by the maxilla and still appears truncated posteriorly. The pattern of the cheek region in plesiosaur skulls with a posterior projection of the maxillary bone (Romer 1956; Brown 1981) again does not suggest a paedomorphic reduction of the jugal. The Sauropterygia show variations in the morphology of the lower cheek region that might well have resulted from a ventral emargination of the cheek region rather than from a reduction of the lower temporal arcade of a fully diapsid reptile. Indeed, the ventral emargination of the cheek produces a great variety of shapes of the jugal bone in turtles (Romer 1956, 1968*a*; Gaffney 1979). This argument may further be supported by reference to the Placodontia where the lower temporal region is either closed (*Placodus* (Sues 1987*b*)), or emarginated to a variable degree (*Placochelys*, *Henodus*). If placodonts are to be classified with the Diapsida (Sues 1987*b*), the ventral emargination of the cheek region would have to be admitted as a mechanism of dermatocranial reduction in this group unless it were assumed that the lower cheek region became secondarily closed in different patterns. At any rate, it may be concluded that the cladistic analysis supports a diagnosis of the Diapsida by the presence of an upper temporal fossa only, bounded ventrally by the postorbital (postorbitofrontal) and squamosal. The pattern of reduction in the ventral cheek region is variable and implies convergences or reversals or both, whatever classification of the diapsid taxa is accepted. This incongruence in pattern might also indicate some incongruence of mechanisms of reduction in the lower temporal region.

The cladistic analysis presented above shows the slender and sigmoidally curved femur to characterize the Neodiapsida (Benton 1985) as well as Araeoscelis. The rather short and stout proximal limb bones of sauropterygians must therefore be interpreted as a secondary development, most probably in adaptation to aquatic locomotion. The absence of an ossified olecranon on the ulna characterizes the sauropterygians and the placodonts as well as the aquatic genus *Claudiosaurus*, and it may be explained by skeletal paedomorphosis (DeRicqlès 1975; Fabre 1981; Rieppel 1987*b*) which is frequently observed in aquatic reptiles. Terrestrial lepidosaurs have developed a specialized epiphysis on the ulna (Haines 1969).

The development of a retroarticular process and of a posteriorly excavated quadrate characterizes the Neodiapsida, including the Placodontia and the Sauropterygia. It is conceivable that these osteological characteristics are correlated with the development of an impedance-matching middle ear, even if the actual structure of the stapes is extremely poorly known in the taxa included. Character distribution indicates that the efficient conduction of high frequency air-borne sound was secondarily lost in non-pachypleurosaur sauropterygians, perhaps yet another adaptation to the aquatic environment (see below).

The status of the Pachypleurosauridae within the Sauropterygia

The above character analysis shows the Pachypleurosauridae to constitute a monophyletic assemblage, characterized by the loss of the ectopterygoid. Other features that have been cited in support of the monophyly of the Pachypleurosauridae are the small upper temporal fossa (Sues & Carroll 1985; Schmidt 1987) and the exclusion of the postorbital from the margin of the upper temporal fossa (Schmidt 1987). However, the postorbital enters the upper temporal fossa in *Anarosaurus* (Nopcsa 1928; Carroll 1981), *Dactylosaurus* (Sues & Carroll 1985), *Keichousaurus* (Young 1958) and variably in the Monte San Giorgio taxa including *Serpianosaurus*, *Neusticosaurus* and *Pachypleurosaurus* (Carroll & Gaskill 1985).

The small upper temporal openings have been cited as a pachypleurosaurid synapomorphy by Sues & Carroll (1985, p. 1608), whereas the same character was interpreted as primitive by Carroll & Gaskill (1985, p. 361). In fact, the relative size of the upper temporal fossa (compared with the diameter of the orbit and with total skull length) as observed in *Anarosaurus* and *Dactylosaurus* falls into the range of ratios shown by *Petrolacosaurus*, *Araeoscelis*, *Claudiosaurus* and *Youngina*. For example, the upper temporal fossa of *Dactylosaurus* corresponds to about 17% of the skull length (based on Sues & Carroll (1985)) compared with 13% of the skull length in *Petrolacosaurus* or 11% in *Youngina*. The above-mentioned genera thus represent the plesiomorph stage of differentiation of the upper temporal fossa, correlated with a relatively slender and triradiate postorbital. In other pachypleurosaurs, including the genera *Serpianosaurus*, *Neusticosaurus* and *Pachypleurosaurus*, the upper temporal fenestra is reduced in size, averaging less than 40% of the diameter of the orbit and less than about 8% of the total skull length. By the reduction of the upper temporal fenestra, the postorbital assumes a more plate-like shape. The reduced size of the upper temporal opening thus characterizes a less inclusive group, subordinated to the Pachypleurosauridae. The implication of the above argument is that non-pachypleurosaur Sauropterygia are characterized by a synapomorphic increase in size of the upper temporal fossa, correlated with the loss of the triradiate shape of the postorbital.

A last feature that might be of potential use in the characterization of the Pachypleurosauridae is the type of suspension of the tympanum. In typical lepidosauromorph reptiles such as extant lizards, the lower edge of the tympanum is attached to the retroarticular process of the lower jaw. In the pachypleurosaurids from the Monte San Giorgio, the quadrate develops a posterior ventral projection for the suspension of the ventral part of the tympanum; this posterior quadrate projection fits into a groove on the retroarticular process upon jaw opening.

A basal dichotomy has been recognized within the Sauropterygia since Nopcsa's (1928) review, subdividing the 'nothosaur' genera into two main groups, the Pachypleurosauridae and the 'Nothosauridae' (paraphyletic (Sues 1987*a*)). This basal dichotomy of the 'nothosaurs' was further emphasized by Peyer (1934) and von Huene (1948, 1956), who considered the pachypleurosaurs to represent an 'early offshoot' from 'true nothosaurs such as *Nothosaurus*...' (von Huene 1956, p. 382). The basal dichotomy within the Sauropterygia is still accepted in the work of Sues & Carroll (1985) and Sues (1987*a*), who recognize the Pachypleurosauridae as a monophyletic clade, representing the relatively plesiomorphous sister group of all other Sauropterygia.

The same conclusion is borne out by the present analysis. The pachypleurosaurs are plesiomorphous with respect to several characters compared with other 'nothosaur' genera: they share the posteriorly excavated quadrate and the presence of a retroarticular process with other neodiapsid and lepidosauromorph taxa as well as with placodonts, their sacrum never incorporates more than four vertebrae (three is the usual number; with only two sacral vertebrae in *Keichousaurus* (Lin, quoted in Sues (1987*a*)); the humerus is rather straight and the upper temporal fossa remains smaller than the orbit.

If the Pachypleurosauridae are accepted as the relatively primitive sister group of all other sauropterygians, an interesting pattern obtains with respect to the morphology and function of the jaw apparatus. Comparing the pachypleurosaur genera *Anarosaurus*, *Dactylosaurus*, *Keichousaurus*, *Neusticosaurus*, *Pachypleurosaurus*, *Serpianosaurus* and *Psilotrachelosaurus* with other genera included in the paraphyletic 'Nothosauridae' by Peyer (1934), namely *Ceresiosaurus*, *Lariosaurus*, *Nothosaurus*, *Paranothosaurus*, *Proneusticosaurus*, *Simosaurus* and *Pistosaurus*, two strikingly different skull patterns obtain.

The pachypleurosaurid skull is less depressed than that of other 'nothosaur' genera; the orbits are relatively large, but the supratemporal fossae remain small. The postorbital region of the skull is not distinctly elongated, and the quadrate only slightly slants backwards: the mandibular joint was situated at the level of or slightly in front of the occipital condyle. The quadrate is concave posteriorly, and most probably supported a tympanic membrane.

This pachypleurosaur pattern will now be compared with the structure shown by *Simosaurus*. The choice of *Simosaurus* for comparison is justified on the following grounds. Sues (1987*a*) classified *Simosaurus* as the sister-group of all other, non-pachypleurosaur sauropterygians. Its skull is known from well-preserved and acid-prepared specimens, which permits a reconstruction of the pattern of arrangement of the jaw adductor musculature. This pattern may be similar in other non-pachypleurosaurid 'nothosaurs' that show modifications of skull proportions differing in detail from those observed in *Simosaurus* but resulting in similar if not even more extreme effects in the reorganization of the jaw adductor musculature.

The following description is based on the skull of *Simosaurus gaillardoti* H. von Meyer, from the *Hauptmuschelkalk* (Upper Muschelkalk, Triassic) of Neidenfels near Crailsheim (Baden–Württemberg, Germany) representing the original specimen of Jaekel's (1905) description. Von Huene (1921) redescribed the specimen, which was subsequently reprepared so as to expose the braincase, described by von Huene (1952). Kuhn-Schnyder (1961) used the same specimen after acid preparation for a discussion of some details of cranial anatomy.

The skull of *Simosaurus* is depressed compared with that of pachypleurosaurs, but not to the same degree as in more advanced 'nothosaurs'. The postorbital region of the skull is elongated; the upper temporal openings have become enlarged, their diameter exceeding that of the orbit. The quadrate of *Simosaurus* slants posteroventrally, carrying the lower jaw joint to a position well behind the occipital condyle. The insertional areas for the jaw adductors (margins of the temporal fossa, lateral wall of the braincase, dorsal surface of the pterygoid), however, all lie in front of the level of the occipital condyle and of the jaw articulation (figure 15*a*). This dictates an inclination of the resultant force vector of the jaw adductor muscles in a posteroventral–anterodorsal direction.

The general arrangement of the jaw adductor musculature thus appears to be distinctly different from that of other reptiles (figure 15*b*). Most reptiles, including the primitive captorhinids (see Carroll 1969*b*), correspond to the pattern termed the 'static pressure system' by Olson (1961), with the jaw adductor muscles arranged such that the resultant force vector is orientated vertically or with a posterodorsal inclination. Maximum force is exerted on the jaws as the latter approach closure.

The alternative pattern was called 'kinetic inertial' by Olson (1961), typical for Palaeozoic amphibians. The jaw adductors are inclined in an anterodorsal–posteroventral direction, exerting maximum force on the lower jaw ramus at wide gape. The result is a snapping bite dependent on the kinetic energy that builds up in the jaws during rapid closure.

At first sight, advanced 'nothosaurs' appear to have returned to the kinetic inertial system, although a proper biomechanical analysis of jaw function is still lacking. It can be approached by a rather crude reconstruction of the pattern of jaw adductor muscle arrangement (figure 15*a*).

The *m. adductor mandibulae externus* is expected to originate from the ventral surface of the postfrontal and of the upper part of the postorbital, from the ventral (medial) surface of the upper temporal arcade, from the anterior surface of the squamosal dorsal to the upper temporal fossa, from the anterior slope of the quadrate (including the posterior adductor) and perhaps from the posteromedial part of the upper temporal fossa.

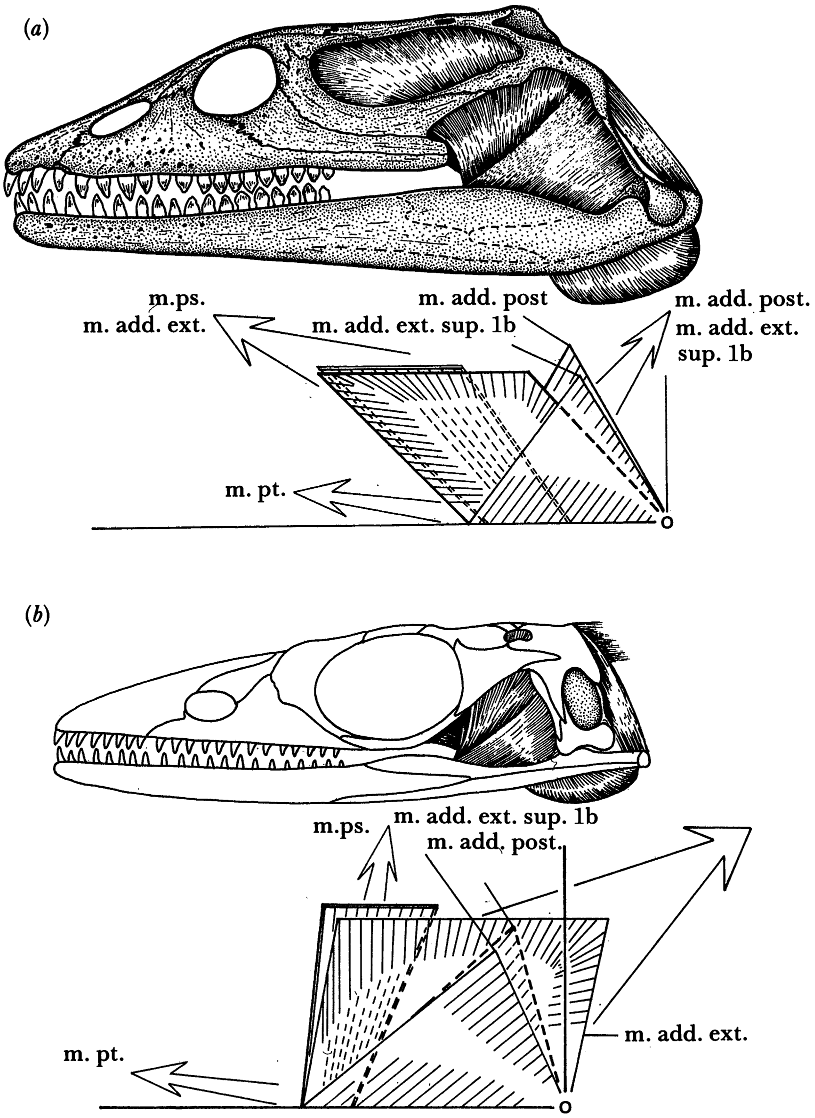

Figure 15. The pattern of jaw adductor musculature in (*a*) *Simosaurus* (skull viewed from a slight dorsolateral angle) compared with (*b*) the pachypleurosaurid pattern (bottom).

With respect to the adductor fossa in the lower jaw, and taking the configuration of the subtemporal fossa into account, the following fibre arrangement must be assumed.

Superficial fibres originating from the lateral edge of the quadrate (posteroventral 1b portion (Rieppel & Gronowski 1981)) as well as superficial fibres from lower edge of the upper temporal arcade must have inserted into the dorsolateral edge of the surangular: an appropriate muscle scar is described by von Huene (1952). Their fibre direction and hence their line of action points in a posterodorsal direction; the mechanical advantage of the muscle portion would have increased with decreasing gape.

Assuming a bodenaponeurotic tendon to be attached to the lateral edge of the adductor fossa on the inner side of the lower jaw, a pinnate structure of the external adductor can be assumed: fibres originating anteriorly, i.e. from the anterior area of the upper temporal fossa, would converge on the tendon in a posteroventral direction, whereas fibres originating from the quadrate, squamosal and posteromedial edge of the upper temporal fossa would run in an anteroventral direction. Such an arrangement presupposes a lateral septum to a parasagittal bodenaponeurosis, the dorsal surface receiving the anterior fibres, the ventral surface receiving the posterior fibres, or a transverse orientation of the bodenaponeurosis instead: the latter arrangement is not very plausible, however, because it would presuppose a distinct coronoid process. The bulk of fibres inserting into the bodenaponeurosis would comprise the medial and deep portions of the external adductor, with a line of action pointing in an anterodorsal direction. The mechanical advantage of this part of the musculature would have become increased with increasing gape.

The *posterior adductor*, deriving from the external adductor ontogenetically, would originate from the deep part of the anterior slope of the quadrate. Indeed, the anterior surface of the posteroventrally inclined quadrate shows a weak ridge running in the longitudinal direction of the bone, which may have separated more superficial fibres inserting into the dorsolateral and dorsal surface of the surangular from the deeper fibres constituting the posterior adductor. The adductor fossa on the lower jaw is wide and deeply emarginated, indicating a massive development of the posterior adductor similar to that observed in crocodiles (Schumacher 1973, fig. 21). Its orientation would have resulted in a force acting in a posterodorsal direction: its adductive force would have increased with the jaws coming near to closure.

The *m. pseudotemporalis* may be assumed to have originated from the medial margin of the upper temporal fossa, from its anteromedial corner, and from the sphenethmoid as well as from the membranous sidewall of the braincase. Because of the circumference of the subtemporal fossa, the orientation of the fibres originating from the parietal complex would point strongly (anterior) or weakly (posterior) in a posteroventral direction: their adductive force would be greatest with the jaws depressed to a variable degree.

The *m. pterygoideus* was probably again well-developed. The quadrate ramus of the pterygoid shows a distinct ventrolateral ridge, which may have separated the origin of the pterygoid muscle (below) from that of the constrictor internus dorsalis muscle (if present) above. The origin of the pterygoideus muscle may have extended anteriorly from the quadrate ramus of the pterygoid on to the posteromedial part of the concave dorsal surface of its palatal shelf. The main orientation of the *m. pterygoideus* is such that it would impart greatest force on the lower jaw ramus at wide gape.

This brief consideration of the arrangement of jaw adductors indicates that the dichotomy between a static pressure system and a kinetic inertial system as described by Olson (1961) is too simplistic to account for jaw mechanics in *Simosaurus*. The posterior displacement of the lower jaw joint carries the adductor fossa of the lower jaw to a position below the posteriormost part of the upper temporal fossa and below the squamosal bone (dorsal suspension of the quadrate). This skull construction effects a functional partitioning of the jaw adductor muscle complex into an essentially anterior division, imparting maximum force on the lower jaw at wide gape, and an essentially posterior complex imparting maximum adductive force on the jaw as it comes near to closure. The anterior complex includes those external adductor fibres originating from the upper temporal arcade and from the anterior part of the upper temporal fossa, as well as the pseudotemporalis and pterygoideus muscles. The posterior complex combines fibres from the posterior third of the upper temporal fossa as well as those originating from the anterior slope of the quadrate and from the lower surface of the squamosal. This complex is assumed to include a well-developed posterior adductor.

The same basic arrangement as reconstructed for *Simosaurus* must also be expected in other non-pachypleurosaur 'nothosaurs': these genera may show an even more depressed skull, resulting in an even more acute angulation of fibre direction relative to the long axis of the lower jaw, either in an anterodorsal, or in a posterodorsal direction. Such fibre angulation is necessary in a strongly depressed skull: vertically orientated fibres would be too short to permit a functional gape because the range of excursion of a muscle fibre within a reasonable range of the length–tension curve depends on its absolute length. Fibre angulation relative to the long axis of the lower jaw not only results in an elongation of individual muscle fibres, but also in a reduced passive extension during jaw depression (Rieppel & Gronowski 1981).

The functional partitioning of the jaw adductor musculature is less pronounced in pachypleurosaurids (figure 15*b*); their skull is of more conventional proportions, with the adductor fossa of the lower jaw lying below the temporal region. The superficial external adductor fibres originating from the anterior slope of the quadrate, as well as the posterior adductor, have a posterodorsally orientated line of action. The medial and deep portions of the external adductor, originating from the roofing of the temporal region, but also from the circumference of the posttemporal fossa lying deep to the quadrate must again have inserted in a bodenaponeurotic tendon system resulting in a resultant force vector pointing in a posterodorsal direction. The anteriorly placed pseudotemporalis muscle must have had a rather vertical orientation, whereas the pterygoideus muscle would have imparted maximal force on the lower jaw ramus at wide gape. This muscle arrangement corresponds to the classical 'static pressure system' as described by Olson (1961), which is plesiomorph at the level of the Reptilia (Carroll 1969*b*).

Jaw mechanics of non-pachypleurosaurid 'nothosaurs' thus appear to have advanced over the plesiomorph condition of the static pressure system primarily by the addition of a strong anterodorsally directed force component. This force component imparted greatest momentum on the lower jaw ramus at wide gape: together with the pterygoideus muscle it provided a means for rapid jaw closure, i.e. for a snapping bite. At the same time, the posterodorsally acting force component was retained to exert momentum on the lower jaw ramus as the latter comes near to closure. The requirement for a rapid bite may reflect different modes of life of non-pachypleurosaur nothosaurs as opposed to pachypleurosaurs. This may also be indicated by the enlargement of the anterior teeth in non-pachypleurosaurid sauropterygians.

A NOTE ON LIFE HISTORY

The dentition of pachypleurosaurs shows little specialization; the anterior teeth are somewhat elongated and weakly point in an anterior direction. Tooth size decreases posteriorly along the jaw ramus. There is no evidence for particular feeding specializations, either in tooth morphology, or in jaw mechanics.

It was argued above that the static pressure system (Olson 1961), plesiomorphous at the level of the Reptilia, was retained in pachypleurosaurs as opposed to other 'nothosaurs' which secondarily developed a kinetic–inertial system. The latter type of jaw mechanism was generally characteristic of most labyrinthodont amphibians; the anthracosaur *Eoherpeton* is one exception to this rule, having developed a static pressure system with other skeletal characteristics suggesting terrestrial habits (Smithson 1980, p. 422). Similarly, the static pressure system was developed in early reptiles, again in correlation to terrestrial habits involving feeding on small and active prey such as insects or other arthropods (Carroll 1969*b*, p. 416). The static pressure system appears appropriate for the manipulation of prey off ground, and for the exertion of occlusal pressure to crush prey items, whereas the kinetic inertial system rather characterizes 'snapping piscivores' (Milner *et al.* 1986, p. 15; see also Panchen 1970, p. 25).

Although this conclusion seems to be based on an empirical generalization (aquatic tetrapods are predominantly characterized by the kinetic inertial system whereas early terrestrial tetrapods developed the static pressure system) there still exists no thorough functional analysis that would explain the function and adaptive significance of these two types of jaw mechanics. This renders the situation unsatisfactory, as the reconstruction of life habits on the basis of these types of jaw systems must remain very conjectural. Taylor (1987, p. 176) thinks that the snapping bite of aquatic tetrapods serves to overcome the drag of the water acting against the jaws by the action of the strong pterygoideus muscle. It has been suggested that modern aquatic reptiles such as crocodiles and the snapping turtle have returned to a static pressure system (Olson 1961, p. 212). However, the snapping turtle (*Chelydra serpentina*) has been shown to perform an aquatic high-speed suction feeding (Lauder 1985, p. 226). The jaw mechanism of *Caiman crocodilurus* was analysed by van Drongelen & Dullemeijer (1982), but no reference was made in this study to the distinction of the static pressure versus the kinetic inertial system introduced by Olson (1961). No recordings were made of prey catching (van Drongelen & Dullemeijer 1982, p. 356), and two types of biting were distinguished during mastication. Noteworthy aspects are the opening of the jaws by elevation of the upper jaw rather than by depression of the mandible, and the early contraction of the pterygoideus anterior muscles during closure of the wide open mouth (van Drongelen & Dullemeijer 1982, p. 356). For all that the comparison with other early tetrapods is valid, it can still be claimed, however, that aquatic feeding specializations are more pronounced in non-pachyplerosaurid 'nothosaurs' than in the Pachypleurosauridae proper.

The Pachypleurosauridae again show little specialization for deep diving. In general, reptile physiology permits an invasion of the aquatic environment with little or no major adaptive changes (Dawson *et al.* 1977; Seymour 1982; Bartholomew 1987). However, the morphology of pachypleurosaurs indicates that their diving abilities may even have been limited by the morphology of their middle ear (Carroll & Gaskill 1985, p. 364).

It was noted above that the quadrate of pachypleurosaurs is deeply excavated posteriorly, providing space for the suspension of a large tympanum between the squamosal dorsally, and the quadrate anteriorly and ventrally. The presence of a large tympanum implies an impedance-matching sound conduction mechanism through an air-filled middle-ear cavity. Deep dives must cause a drop of relative pressure within the middle ear cavity, resulting in the danger of rupture of the tympanic membrane. This is why most aquatic reptiles and mammals show some adaptation to diving in their middle-ear structure.

In the marine turtle *Chelonia mydas*, the tympanic membrane is lacking; the extracolumella is connected to a heavy fibrous cutaneous plate instead. The lateral tympanic cavity in the funnel-shaped quadrate bone is not filled with air as in terrestrial turtles, but with a 'fatty material' (Ridgeway *et al.* 1969, p. 886). Mosasaurs have convergently developed a turtle-like suspension of the tympanic membrane on a funnel-shaped quadrate bone: some genera have been reported to show a partly calcified tympanum, which probably prevented its rupture during rapid dives (Russell 1967, p. 59). A further problem created by the aquatic environment is that the impedance mismatch between external environment and inner ear is only slight: there is therefore no need for an impedance-matching middle-ear transformer. Accordingly, aquatic mammals (otariid seals) show a reduction in size of the tympanum but an increased size of the oval window, resulting in a ratio of 10:1 rather than 35:1 to nearly 50:1 as compared with their terrestrial relatives (fissiped carnivores) (Repenning 1972, p. 315). In addition, seals have the ability to close the external auditory meatus, and at diving depths of 80–100 m or more a blood-flooded cavernous tissue expands in the middle-ear cavity, supporting the tympanic membrane and compensating for the increasing drop in pressure within the middle-ear cavity (Repenning 1972; see also Ramprashad *et al.* 1972). Unfortunately, there are no investigations of adaptations of the middle-ear structure to diving habits in the 'marine' Galapogos iguana *Amblyrhynchus*. It would be of great importance for a proper interpretation of marine reptiles to have some data on the relative size of the tympanic membrane and on the size ratio between the latter and the stapedial footplate compared with terrestrial representatives of this lizard family.

In pachypleurosaurids, there is no indication of any adaptation of middle-ear structure to rapid and deep diving. The surface ratio of the tympanic membrane to the oval window must have been rather large. In extant lizards, the lower edge of the tympanum is attached to the retroarticular process of the lower jaw: depression of the jaw causes the tympanum to fold in its lower part. As the posterior rim of the tympanic membrane is suspended on the fascia of the depressor mandibulae muscle, the tympanum is on the whole rather loosely suspended. In a diving lizard, a decrease in pressure in the middle ear may be compensated to a certain degree (up to a certain diving depth) by the slackness of the tympanic membrane. In pachypleurosaurids, on the other hand, the quadrate was immovably suspended from the squamosum. It also forms a posteroventral projection supporting the lower edge of the tympanic membrane, whereas dorsally the latter was attached to the anterior and posterior descending processes of the squamosum, and to the quadrate bone. This provided a rigid suspension for a taut tympanic membrane, which would seem to have been able to accommodate pressure changes upon diving even less than that of modern lizards.

Pachypleurosaurids do not seem to have been efficient divers. They rather appear to represent a group of generalist feeders living in nearshore areas and staying in rather shallow waters. This accords well with the conclusions of Sues (1987*a*) who interpreted pachypleurosaurs as inhabitants of lagoonal to shallow-water marine environments, swimming mainly by tail propulsion. In *Serpianosaurus* the neural spines are elevated in the posterior dorsal and anterior caudal region of the vertebral column (figure 1), which would have increased the efficiency of tail propulsion. Limb-mediated propulsion seems to have been of lesser importance, as no particular modifications can be identified. If anything, there is a tendency towards some reduction of phalanges rather than the development of hyperphalangy, and sex *x* in particular shows a weak humerus, which would not accord with an interpretation of the forelimbs as hydrofoils.

Depositional conditions in the Monte San Giorgio basin along the margin of the Tethys would support the interpretation of pachypleurosaurs as inhabitants of lagoonal or shallow-water marine environments (Sues 1987*a*), although the precise distance from the coast cannot be indicated. On the whole, the Monte San Giorgio fauna comprises forms ranging from pelagic to terrestrial animals. The chondrostean *Birgeria*, large ichthyosaurs such as *Cymbospondylus*, and large nothosaurs (*Ceresiosaurus*, *Paranothosaurus*) are likely to have inhabited the open sea. Prolacertilians such as *Macrocnemus* and *Tanystropheus*, but also thalattosaurs such as *Clarazia* and *Hescheleria* and perhaps the small ichthyosaur genus *Mixosaurus*, would seem to have lived in nearshore areas, whereas the rauisuchid *Ticinosuchus* represents a terrestrial element in the Monte San Giorgio fauna. *Serpianosaurus* in particular comes from the 'Grenzbitumen' beds, representing a time-span for which the palaeogeography has been worked out in some detail (see summary in Kuhn-Schnyder (1974)). The 'Grenzbitumen' deposits border on the Monte San Salvatore, which represented a reef during the time of transition from the Anisian to the Ladinian. Whether or not this reef was situated close to the coastline, it emerged from the water, itself providing a patch dry land. This conclusion is supported by plant remains ('*Voltzia*') enclosed within the dolomitic limestone layers intercalated between the bituminous shales of the 'Grenzbitumen' horizon.

Circumstantial evidence supporting the interpretation of pachypleurosaurs as inhabitants of nearshore environments comes from the recent description of an embryo of *Neusticosaurus*, which probably indicates ovipary for that group (Sander 1988).

Simosaurus and other non-pachypleurosaurid 'nothosaurs' have altered the shape and position of the quadrate so as to make the suspension of a superficial tympanic membrane impossible. They have given up an impedance-matching sound-conducting mechanism, perhaps in adaptation to deep diving excursions. Elongation of jaws and teeth indicates a piscivorous diet; cephalopods may also have been taken. The rapid snapping bite effected by the reorientation of the jaw adductor musculature provided the means to grab agile prey. As a snapping bite would tend to expel water from the mouth and push prey objects away from the gape, nothosaurs may have attacked prey objects by a sideward jerk of the jaws, as do many long-snouted crocodiles (Seymour 1982).

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KEY TO ABBREVIATIONS USED IN FIGURES

acc	accessory intervertebral articulation	m.pt	m. pterygoideus
an	angular	mt	metatarsal
ap	anterior process of cervical rib	n	nasal
ar	articular	ns	neural spine
as	astragalus	o.f	obturator foramen
c	coronoid	p	parietal
ca	calcaneum	pa	parapophysis
car	caudal rib	p.art	prearticular flange
cb_1	first ceratobranchial	pf	postfrontal
cl	clavicle	pl	palatine
co.f	coracoid foramen	pm	premaxilla
cor	coracoid	po	postorbital
cr	cervical rib	poz	postzygapophysis
d	dentary	prf	prefrontal
di	diapophysis	prz	prezygapophysis
ent.f	entepicondylar foramen	pt	pterygoid
f	frontal	pu	pubis
fe	femur	q	quadrate
fi	fibula	qj	quadratojugal
hu	humerus	ra	radius
hy	hypapophysis	r.art	retroarticular process
icl	interclavicle	sa	surangular
il	ilium	sc	scapula
im	intermedium	sco	scleral ossicles
in	internal naris	so	supraoccipital
is	ischium	sp	splenial
j	jugal	sq	squamosum
m	maxilla	sr	sacral ribs 1–4
m.add.ext.	m. adductor mandibulae externus	ti	tibia
m.add.ext.sup.1b	posteroventral portion of the external adductor	tp	transverse process
		ul	ulna
m.add.post.	m. adductor mandibulae posterior	uln	ulnare
mc	metacarpal	v	vomer
m.ps	m. pseudotemporalis		

APPENDIX 1

Definitions

All measurements were taken on both sides of the animal, if possible; tables A1 and A2 reproduce the mean values of these two measurements.

To determine the *glenoid–acetabulum length*, the distance from the posteromedial corner of the proximal humerus head to the posteromedial corner of the proximal femur head was measured; if the body of the animal is flexed, the mean value was calculated from the measurements of both body sides.

The *standard length* is the length of the four last dorsal vertebrae, be it in dorsal or ventral view. In ventral view the measurement was taken across the vertebral centrum; in dorsal view, the measurement was taken across the pre- and postzygapophysis. A specimen of *Neusticosaurus* prepared from both sides indicates a good agreement between these two methods of measurement.

The *posterior trunk centrum* length was determined on one out of the three or four last dorsal vertebrae in specimens preserving these vertebrae in lateral or ventral exposure.

Head length was determined as the length of the lower jaw ramus, which is often disarticulated and thus allows well-defined measurements.

All measurements are given in millimetres.

Table A1. Size variation in the genus *Serpianosaurus*

(For abbreviations used see p. 73.)

specimen no.	sex	pre-sacrals	cervicals	dorsals	head-length mm	trunk mm	standard mm	humerus mm	hu min mm	hu dist mm	radius mm	ulna mm	metacarp 3 mm	femur mm	tibia mm	fibula mm	metatars 4 mm
T 81	*y*	—	—	—	—	—	—	24.7	5.2	10.9	—	—	—	—	11.1	11.3	7.7
T 96	*x*	—	16	—	43.5	79.0	—	22.7	4.9	7.9	12.6	11.3	5.2	21.7	11.7	12.3	—
T 97	*x*	—	—	—	—	102.9	22.2	25.0	5.4	8.7	14.0	12.1	6.0	25.7	13.9	14.9	—
T 132		—	—	—	26.9	41.0	9.7	7.8	1.6	2.8	5.1	4.9	2.3	9.4	5.3	5.6	3.7
T 951	*x*	37	16	21	43.5	89.8	18.7	18.9	3.6	6.1	12.1	11.2	4.8	20.4	12.2	12.7	—
T 1045	*y*	—	—	—	80.6	187.0	39.2	44.9	7.2	15.8	24.9	22.2	—	40.3	22.0	22.5	14.6
T 1071	*x*	38	18	20	41.9	77.0	18.3	18.2	3.7	6.0	11.6	10.6	4.2	20.7	12.0	13.3	7.9
T 1834 a, b	*y*	—	—	—	—	168.0	—	38.2	6.1	13.6	24.0	20.1	9.4	35.5	19.8	20.2	13.6
T 3402	*y*	—	—	—	—	75.0	—	23.7	3.4	7.7	11.2	11.1	—	20.0	10.6	11.6	7.3
T 3406	*y*	37	14	23	47.5	101.3	24.5	28.0	4.2	11.6	14.8	13.4	7.4	23.9	13.3	14.1	9.4
T 3448	?	—	—	—	—	—	22	—	4.8	—	15.4	13.9	6.4	24.6	13.5	14.3	9.6
T 3473	?	—	—	—	—	—	—	18.1	4.0	—	—	—	—	—	—	—	—
T 3674	*y*	—	—	—	—	60.5	—	19.5	3.3	7.1	10.9	9.3	4.5	18.8	9.8	10.2	—
T 3675	*y*	36	15	21	—	106.6	24.3	30.4	4.4	8.3	16.1	14.3	6.4	27.8	15.2	15.7	—
T 3676	*y*	37	15	22	50.1	101.3	21.6	29.2	5.4	10.1	—	—	5.3	26.0	14.1	14.7	8.7
T 3677	*y*	36	16	20	48.9	86.6	22.1	30.7	4.6	10.6	15.1	14.2	—	25.8	13.6	14.3	9.0
T 3678	*y*	—	—	—	—	—	—	35.4	5.7	12.3	18.1	16.4	7.7	29.6	—	—	10.5
T 3679	*y*	—	—	—	—	—	—	39.6	6.4	12.7	20.8	18.3	—	32.0	17.6	17.7	—
T 3680	?	36	16	20	43.0	81.8	19.1	24.8	4.2	—	—	—	—	22.8	—	—	—
T 3681	*y*	—	16	—	46.9	88	—	29.1	4.1	10.1	15.3	13.4	—	25.8	13.5	—	9.4
T 3682	*y*	37	16	21	—	104.0	—	33.5	5.0	11.4	17.3	15.5	6.7	29.5	15.4	15.6	9.8
T 3683	?	—	—	—	—	—	15.7	19.5	3.6	—	—	9.8	—	18.3	10.8	11.3	—
T 3684	*x*	38	15	23	43.0	81.5	16.8	17.9	3.2	5.5	11.4	10.8	—	19.4	11.4	12.1	7.0
T 3685	*y*	35	15	20	46.0	82.05	19.9	22.4	4.0	—	12.8	11.6	5.2	22.8	12.5	13.0	6.6
T 3709	*y*	—	—	—	60.3	—	—	26.8	4.6	9.2	16.6	15.0	—	—	—	—	—
T 3742	*y*	37	16	21	—	134.5	33.1	48.9	7.8	16.2	25.7	23.2	9.9	43.6	20.6	—	15.3
T 3807	*x*	—	—	—	—	—	—	21.6	3.5	5.9	—	—	—	21.8	—	—	—
T 3810	*x*	—	—	—	—	—	—	13.8	2.4	4.0	8.7	7.6	3.5	18.3	—	—	—
T 3931	*y*	38	15	23	74.5	147.6	30.8	35.7	4.9	11.7	21.2	18.9	7.7	34.8	19.6	20.1	12.2
T 3933	?	37	16	21	—	92.5	20.5	—	—	9.5	14.4	13.4	—	24.3	12.9	13.0	8.5
T 4017 X-ray		—	—	—	—	—	—	—	—	—	—	—	—	19	—	—	—
T 4043 X-ray		—	—	—	—	—	—	—	—	—	—	—	—	22	—	—	—
T 4076 X-ray	*x*	—	—	—	—	—	—	20.0	4.0	6.0	12	10	—	—	—	—	—
T 4115 X-ray	*x*	—	—	—	—	—	—	22.7	4.4	7.6	13.5	11.5	—	—	—	—	—
T 4133 X-ray		—	—	—	—	—	—	—	—	—	—	—	—	18.5	—	—	—

Table A2. Proportions in the genus *Serpianosaurus*

(For abbreviations used see p. 73.)

specimen no.	femur mm	head: trunk	head: standard	hu: trunk	hu: standard	hu min: hu dist	ra: standard	mc3: standard	hu:fe	hu:ra	hu:mc3	ra:ul	hu: hu dist	head: hu	fe:trunk	fe: standard	fib: standard	mt4: standard	fe:fib	fe: mt4	fib:tib
T 81	—	—	—	—	—	0.477	—	—	—	—	—	—	2.266	—	—	—	—	—	—	—	1.018
T 96	21.7	0.551	—	0.287	—	0.620	—	—	1.046	1.802	4.365	1.115	2.873	1.916	0.275	—	—	—	1.764	—	1.051
T 97	25.7	—	—	0.243	1.126	0.621	0.631	0.270	0.973	1.786	4.167	1.157	2.874	—	0.250	1.158	0.671	—	1.725	—	1.072
T 132	9.4	0.656	2.773	0.190	0.804	0.571	0.526	0.237	0.830	1.529	3.391	1.041	2.786	3.449	0.229	0.969	0.577	0.381	1.679	2.541	1.057
T 951	20.4	0.484	2.326	0.210	1.011	0.590	0.647	0.257	0.926	1.562	3.938	1.080	3.098	2.302	0.227	1.091	0.679	—	1.606	—	1.041
T 1045	40.3	0.431	2.056	0.240	1.145	0.456	0.635	—	1.114	1.803	—	1.122	2.842	1.795	0.216	1.028	0.574	0.372	1.791	2.760	1.023
T 1071	20.7	0.544	2.290	0.236	0.995	0.617	0.634	0.230	0.879	1.569	4.333	1.094	3.033	2.302	0.269	1.131	0.727	0.432	1.556	2.620	1.108
T 1834a, b	35.5	—	—	0.227	—	0.449	—	—	1.076	1.592	4.064	1.194	2.809	—	0.211	—	—	—	1.757	2.610	1.020
T 3402	20.0	—	—	0.316	—	0.442	—	—	1.185	2.116	—	1.009	3.078	—	0.267	—	—	—	1.724	2.740	1.094
T 3406	23.9	0.469	1.939	0.276	1.143	0.362	0.604	0.302	1.172	1.892	3.784	1.104	2.414	1.696	0.236	0.976	0.576	0.384	1.695	2.543	1.060
T 3448	24.6	—	—	—	—	—	0.700	0.291	—	—	—	1.108	—	—	—	1.118	0.650	0.436	1.720	2.563	1.059
T 3473	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T 3674	18.8	—	—	0.322	—	0.465	—	—	1.037	1.789	4.333	1.172	2.746	—	0.311	—	—	—	1.843	—	1.041
T 3675	27.8	—	—	0.285	1.251	0.530	0.663	0.263	1.094	1.888	4.750	1.126	3.663	—	0.261	1.144	0.646	—	1.771	—	1.033
T 3676	26.0	0.495	2.319	0.288	1.352	0.535	—	0.245	1.123	—	5.509	—	2.891	1.716	0.257	1.204	0.681	0.403	1.769	2.989	1.043
T 3677	25.8	0.565	2.213	0.355	1.389	0.434	0.683	—	1.190	2.033	—	1.063	2.896	1.593	0.298	1.167	0.647	0.407	1.804	2.867	1.051
T 3678	29.6	—	—	—	—	0.463	—	—	1.196	1.956	4.597	1.104	2.878	—	—	—	—	—	—	2.819	—
T 3679	32.0	—	—	—	—	0.504	—	—	1.238	1.904	—	1.137	3.118	—	—	—	—	—	1.808	—	1.006
T 3680	22.8	0.526	2.251	0.303	1.298	—	—	—	1.088	—	—	—	—	1.734	0.279	1.194	—	—	—	—	—
T 3681	25.8	0.533	—	0.331	—	0.406	—	—	1.128	1.902	—	1.142	2.881	1.612	0.293	—	—	—	—	2.745	—
T 3682	29.5	—	—	0.322	—	0.439	—	—	1.136	1.936	5.000	1.116	2.939	—	0.284	—	—	—	1.891	3.010	1.013
T 3683	18.3	—	—	—	1.242	—	—	—	1.066	—	—	—	—	—	—	1.166	0.720	—	1.619	—	1.046
T 3684	19.4	0.528	2.560	0.220	1.065	0.582	0.679	—	0.923	1.570	—	1.056	3.255	2.402	0.238	1.155	0.720	0.417	1.603	2.771	1.061
T 3685	22.8	0.561	2.312	0.273	1.126	0.526	0.643	0.261	0.982	1.750	4.308	1.103	2.947	2.054	0.278	1.146	0.653	0.332	1.754	3.455	1.040
T 3709	—	—	—	—	—	0.500	—	—	—	1.614	—	1.107	2.913	2.250	—	—	—	—	—	—	—
T 3742	43.6	—	—	0.364	1.477	0.481	0.776	0.299	1.122	1.903	4.939	1.108	3.019	—	0.324	1.317	—	0.462	—	2.850	—
T 3807	21.8	—	—	—	—	0.593	—	—	0.991	—	—	—	3.661	—	—	—	—	—	—	—	—
T 3810	18.3	—	—	—	—	0.600	—	—	0.754	1.586	3.943	1.145	3.450	—	—	—	—	—	—	—	—
T 3931	34.8	0.505	2.419	0.242	1.159	0.419	0.688	0.250	1.026	1.684	4.636	1.122	3.051	2.087	0.236	1.130	0.653	0.396	1.731	2.852	1.026
T 3933	24.3	—	—	—	—	—	0.702	—	—	—	—	1.075	—	—	0.263	1.185	0.634	0.415	1.869	2.859	1.008
T 4017 X-ray	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T 4043 X-ray	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T 4076 X-ray	—	—	—	—	—	0.667	—	—	—	1.667	—	1.200	3.333	—	—	—	—	—	—	—	—
T 4115 X-ray	—	—	—	—	—	0.579	—	—	—	1.681	—	1.174	2.987	—	—	—	—	—	—	—	—
T 4133 X-ray	18.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Key to abbreviations used in tables

head	head length
trunk	glenoid–acetabulum length
standard	standard length
humerus, hu	humerus length
hu min	minimal width of humeral shaft
hu dist	width of distal head of humerus
femur, fe	femur length
radius, ra	radius length
ulna, uln	ulna length
metacarp 3, mc3	length of 3rd metacarpal
tibia, tib	tibia length
fibula, fib	fibula length
metatars 4, mt4	length of 4th metatarsal
p.t.c.	length of posterior trunk vertebra

Figure 1. The type specimen of *Serpianosaurus mirigiolensis* n. gen. n. sp.